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Systematics and Evolutionary Relationships of Spiny Pocket Mice, Genus Liomys

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INTRODUCTION

Spiny pocket mice of the genus *Liomys* are members of the rodent family Heteromyidae and together with the genus *Heteromys* form the subfamily Heteromyinae. Their geographic range extends from northern Sonora, in western México, and southern Texas southward to the vicinity of the Panamá Canal Zone. Within this area, members of the genus occur mainly in dry to arid situations being replaced in areas of rain forest and cloud forest by members of the genus *Heteromys*. The vernacular name for *Liomys* is based on the fact that many of their hairs have been modified in the form of stiff, aristiform spines. However, my field companions have other names for members of the genus such as "green mice" and others that would not be appropriate to publish, because of the tendency of these rodents to rot quickly after being trapped and because their thin skin tears easily during preparation.

Although spiny pocket mice are relatively common inhabitants of much of México and Central America, it was not until 1868 that representatives of the genus were described and not until 1902 that the generic name was proposed. Gray (1868) described the first two species that are presently included in the genus *Liomys,* although he placed them in the genus *Heteromys* Desmarest, 1817, where they remained until the genus *Liomys* was described. The two species (*Heteromys irroratus* and *Heteromys albolimbatus*) were based on only three specimens from Oaxaca—the holotype of *irroratus* from an unspecified locality in the state and the two specimens of *albolimbatus* from La Parada. A third species (*Heteromys adspersus*), now assignable to *Liomys,* was described by Peters (1874) from Panamá. These three species together with other species of *Heteromys* known at the time were reviewed by Alston (1879-82) who recognized only two species, *Heteromys desmarestianus* and *Heteromys longicaudatus,* in México and Central America. The species *irroratus, albolimbatus,* and *adspersus* were placed in the synonymy of *H. longicaudatus.* A fourth species (*Heteromys alleni*) was described by Coues (*in* J. A. Allen, 1881:187-89) based on a specimen from Río Verde, San Luis Potosí, although Allen in the same paper expressed some doubt as to the validity of the species in view of Alston's findings. Later, however, Allen (1891:268-272) concluded on the basis of additional specimens from Brownsville, Texas, and Moroleón, Guanajuato, that *Heteromys alleni* was a valid species. The next descriptions of members of the genus appeared in 1893 when Thomas (1893*a*:329-32, 1893*b*:233-34) named three species—*Heteromys bulleri, H. salvini, H. pictus*—and a subspecies of *H. salvini.* In the first of these papers Thomas recognized all species named to that time and suggested that species of the genus could be defined by a combination of the characteristics based on number of plantar tubercles and hairy or naked soles of hind feet. Four years later, J. A. Allen (1897) described another species, *Heteromys hispidus*, from Compostela, Nayarit, and listed known members of the genus, dividing them into three groups based on Thomas' characteristics. It is of interest to note that Allen inadvertently omitted from his listing *Heteromys pictus* Thomas, 1893, with which *hispidus* is now considered synonymous.

The genus *Liomys* was formally described in 1902 by C. H. Merriam with *Heteromys alleni* Coues as the type species. *Liomys* was distinguished from *Heteromys* by Merriam mainly on the basis of the absence of secondary lobes or permanent enamel islands on the molars of *Liomys* that are present in *Heteromys*. In the same paper, Merriam described 11 new species and four new subspecies of *Liomys* and also *Heteromys annectens*, which is now considered to be a member of the genus *Liomys*. The following year Elliot (1903*a*:146-47, 1903*b*:233) described two new species, one from Morelos (*Heteromys exiguus*) and the other from Veracruz (*Heteromys paralius*). In these two papers as in his other major works of the next several years, Elliot (1904:368-82; 1905:316-23; 1907:344-47) considered *Liomys* to be a subgenus of *Heteromys*. Goldman (1904:82) characterized a species, *Liomys parviceps*, from Michoacán and in so doing accorded *Liomys* generic rank. In the next four years, J. A. Allen (1906:211, 251, 1908: 652) described two new species and a new subspecies (*Heteromys jaliscensis*, *Heteromys vulcani*, *Heteromys pictus escuinapae*), and placed them in the genus *Heteromys* without commenting on the status of *Liomys*.

Therefore, by 1911 when Goldman's comprehensive work, "Revision of the spiny pocket mice (genera Heteromys and Liomys)" appeared, 25 species and five subspecies were recognized in the genus. Goldman recognized nine species and 17 subspecies, besides the nominal races, based upon his study of 1003 specimens. In addition, he described one new species, *Liomys guerrerensis*, from Omilteme, Guerrero, and one new subspecies, *Liomys irroratus pretiosus*, from Metlaltoyuca, Puebla. Although Goldman did not accord them subgeneric rank, he did divide the genus into three species groups—*irroratus* group, *pictus* group, and *crispus* group. This was the last major work to appear dealing with Recent species of the genus until 1948, although in the intervening years descriptions of one species, *Liomys anthonyi* (Goodwin, 1932*a*:2), and three subspecies—*Liomys salvini aterrimus* (Goodwin, 1938:4), *Liomys irroratus pullus* (Hooper, 1947: 47), *Liomys irroratus acutus* (Hall and Villa, 1948:253)—appeared, and *Liomys vulcani* was reduced to subspecific status under *Liomys salvini* (Goodwin, 1946: 374). In 1948, Hooper and Handley (1948) presented a synopsis of the known races of *Liomys irroratus* and analyzed the trends in geographic variation within the species. Since 1948, the only papers dealing with the taxonomy of the genus were a description of a new species, *Liomys pinetorum* (Goodwin, 1956*b*:2-3), from Chiapas and a new subspecies, *Liomys irroratus yautepecus* (Goodwin, 1956*a*:7-8), from Oaxaca; the latter was subsequently arranged as a synonym of *L. i. irroratus* (Goodwin, 1969:148). The only nominal fossil member of the genus is *Liomys centralis* described by Hibbard (1941*a*:349) from the Rexroad

Fauna of western Kansas, although other fossil and subfossil material has been reported from San Josecito Cave, Nuevo León, by Cushing (1945:185) and Jakway (1958:320), and from caves in southern Tamaulipas by Koopman and Martin (1959:2, 6) and Dalquest and Roth (1970:226). Therefore, at the beginning of my study 11 Recent species, 22 Recent subspecies, and one fossil species were recognized in the genus.

The purpose of this study was first to examine the taxonomic relationships of the species of the genus *Liomys* and, after forming a new systematic arrangement of the taxa, to examine the evolutionary relationship of the species within the genus and to evaluate their relationships to members of the genus *Heteromys*. The present work is easily divisible into three sections—nongeographic variation, geographic variation, and an assessment of evolutionary relationships—although no one section is independent from the other two. The section on nongeographic variation examines variation with age, secondary sexual variation, individual variation, and variation resulting from molt. Study of geographic variation and specific relationships using both univariate and multivariate statistics has shown that only four of the 11 species recognized prior to this study are actually distinct; these species are *Liomys irroratus* (seven subspecies), *Liomys pictus* (four subspecies), *Liomys salvini* (three subspecies), and *Liomys adspersus* (monotypic). In addition to these four species, one other monotypic species, *Liomys spectabilis*, recently described by me (Genoways, 1971) is recognized, resulting in a total of five species within the genus. Because a fossil record of the genus is nearly nonexistent, I have attempted to analyze the relationships of these five species to each other and to members of the genus *Heteromys* by study of such characteristics as external and cranial morphology, structure of unworn premolars and molars, bacular morphology, morphology of glans penes, comparative karyology, sperm morphology, ectoparasite faunas, structure of pterygoid bone, pelage characteristics, morphology of hind feet, and reproductive patterns. The section on specific relationships also should be used as an appendix to the section on geographic variation because all of these same characteristics were used in determining the species to be recognized. I decided to place all of the specific characteristics in a single section for ease of comparison rather than scattering them throughout the sections on geographic variation within the accounts of individual species.

METHODS, MATERIALS, AND ACKNOWLEDGMENTS

Discussed here are the methods and materials used in the analysis of nongeographic and geographic variation or related to more than one part of the section on evolutionary relationships. Specific methods and materials used in individual parts of the section on evolutionary relationships are detailed in introductory remarks to each of the parts.

In the course of this study, 7186 specimens representing the five species of the genus *Liomys* were examined. The vast majority of these specimens were standard museum skins and skulls accompanied by the appropriate field data. Additional material consisted of complete skeletons, skins without skulls, skulls unaccompanied by skins, and specimens preserved in alcohol. All of the holotypes of nominal taxa of *Liomys* were examined except those of *Liomys adspersus*, *Liomys irroratus*, *Liomys albolimbatus*, *Liomys salvini*, *Liomys salvini nigrescens*, and *Liomys pictus*, although the latter five were kindly examined in the British Museum (Natural History) for me by Dr. J. Knox Jones, Jr. The holotype of *Liomys adspersus*, which supposedly is deposited in the Berlin Museum, was beautifully figured by Peters (1874) in his original description.

From most adult specimens and from selected individuals of other age categories four external measurements and weight were recorded from the specimen labels and 10 cranial measurements were taken by means of dial calipers. In order to clarify exactly in what manner measurements were taken, I have defined each below; letters in parenthesis are used to identify the measurement in some figures. All measurements in text are given in millemeters unless otherwise noted.

Total length (TL).—Distance from tip of nose to tip of fleshy part of tail; recorded by preparator.

Length of tail (TV).—Distance from joint between proximal tail vertebrae and sacrum to fleshy tip of tail; recorded by preparator.

Length of hind foot (HF).—Distance from tip of longest claw to heel; recorded by preparator.

Length of ear.—Distance from bottom of notch to distalmost edge of fleshy part of ear; recorded by preparator; not used in analysis of nongeographic or geographic variation.

Weight.—Total weight recorded in grams by preparator; not used in analysis of nongeographic or geographic variation.

Greatest length of skull (GLS).—From A to B in Fig. 1; greatest distance from the anteriormost projection of the nasal bones to the posteriormost portion of the occipital bone.

Zygomatic breadth (ZB).—From C to D on Fig. 1; greatest width across zygomatic arches at right angle to longitudinal axis of cranium.

Interorbital constriction (IOC).—From E to F on Fig. 1; least width across the interorbital constriction at right angle to longitudinal axis of cranium.

Mastoid breadth (MB).—From G to H on Fig. 1; greatest width across mastoid processes at right angle to the longitudinal axis of cranium.

Length of nasals (LN).—From A to I on Fig. 1; greatest distance from anteriormost projection of nasal bones to the posteriormost projection of the nasals along their medial suture.

Length of rostrum (LR).—From A to J on Fig. 1; greatest distance from notch lateral to lacrimal bone to anteriormost projection of nasal bone on the same side of the cranium.

Length of maxillary toothrow (MTR).—From K to L on Fig. 1; distance from anterior lip of alveolus of the premolar to the posterior lip of the alveolus of M3.

Depth of braincase (DBC).—From M to N on Fig. 1; least distance from basioccipital-basisphenoid complex to dorsalmost portion of cranium.

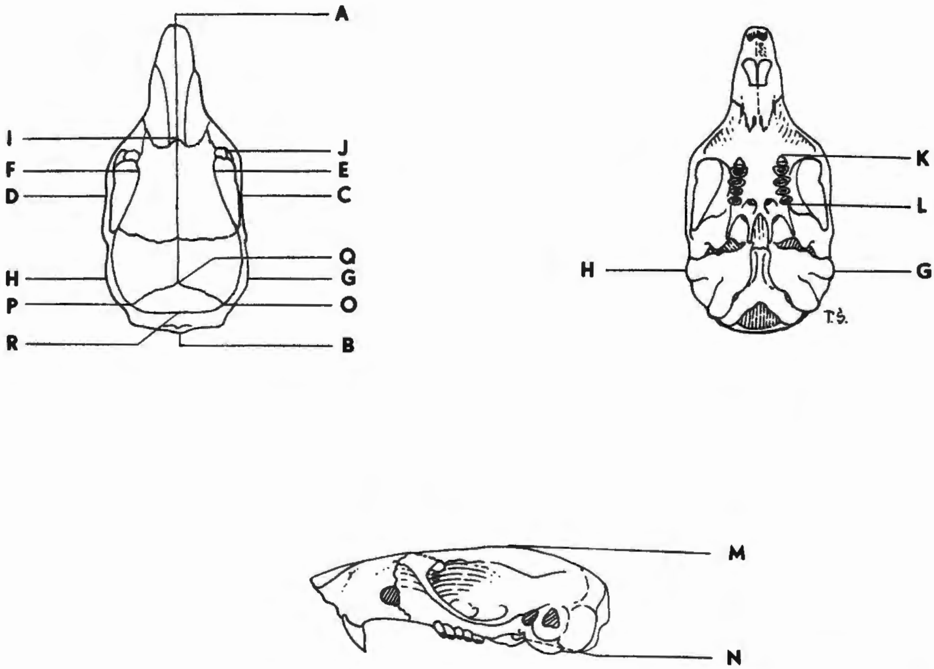

FIG. 1.—Skull of *Liomys pictus* illustrating points between which measurements described in text were taken.

Interparietal width (IW).—From O to P on Fig. 1; greatest transverse width measured from the lateralmost projections of the interparietal bone at right angle to longitudinal axis of cranium.

Interparietal length (IL).—From Q to R on Fig. 1; greatest distance from anteriormost projection of interparietal bone to posteriormost border of interparietal bone; this measurement was always taken along medial line of cranium even when there was a notch in posterior border.

Variation in color was studied by use of a Photovolt Photoelectric Reflection Meter, Model 610, on which reflectance values are recorded as a percentage of pure white (see Lawlor, 1965; Dunnigan, 1967). Readings of color reflectance for red, green, and blue were taken in the middorsal region of specimens with unworn pelage. Study of variation in color was extremely difficult for several reasons. Although I attempted to use specimens collected only in June, July, August, and September, those from many critical areas were collected at other times of the year, thus forcing me to use material obtained in several other months. Another problem encountered was that many critical specimens were collected by Nelson and Goldman in the late 1890's and early 1900's whereas many others have been collected since 1950; the possible changes in color resulting from long-term museum storage, even under the best of circumstances, is unknown. The conditions under which specimens are housed at various museums introduces still another variable. Results of my analysis of variation in color should be viewed, therefore, with these variables in mind.

Four qualitative cranial characters were recorded and scored for each adult and subadult specimen examined for inclusion in the analysis of geographic variation. Some authors (Berry and Searle, 1963; Hedges, 1969) have termed these "epigenetic polymorphism"; however, I have avoided use of this term because I felt epigenetic polymorphism carried connotations that could not be proven on the basis of my data. Three of these characters (shape of posterior termination of nasal bone, length of nasals in comparison with length of premaxillae, and condition of the posterior margin of the interparietal bone) were used by Goldman (1911) in his analysis of *Liomys*; the fourth was based upon my observation that some individuals had the interparietal divided, whereas others did not. Another character (shape of interparietal bone) was used by Goldman, but I found this character to be so variable that it was unsatisfactory for analysis. The states for each of these characters, together with the score used in the analysis (see Fig. 2), are as follows: shape of posterior margin of nasals—emarginate (1), rounded (2), truncate (3); length of premaxillary bones—longer than nasals (1), equal to nasals (2); condition of interparietal bone—undivided (1), divided (2); posterior margin of interparietal bone—notched (1), slightly notched (2), unnotched (3).

Statistical procedures requiring computer analyses were performed on the GE 635 computer at The University of Kansas; simpler procedures were carried out on the Olivetti Underwood Programma 101 in the Museum of Natural History of Kansas. Univariate analyses of geographic variation were performed using a program (UNIVAR) written and extensively used by Power (1970). This program yields standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) and, when two or more groups are being compared, employs a single-classification analysis of variance or anova (*F*-test, significance level .05) to test for significant differences between or among the means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) developed by Gabriel (1964) was used to determine maximally nonsignificant subsets.

Multivariate analyses were performed using the NT-SYS programs developed at The University of Kansas by F. J. Rohlf, R. Bartcher, and J. Kishpaugh. In all multivariate analyses, the OTUs were grouped localities discussed below and the values for each character were means for the measurement or mean score for qualitative cranial characters. Matrices of Pearson's product-moment correlation were computed, and phenetic distance coefficients were derived from standardized character values. Cluster analyses were conducted using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices and a phenogram was generated for each. Phenograms were compared with their respective matrices, and a coefficient of cophenetic correlation was computed for each comparison; I have shown only the phenetic distance phenograms because their coefficients of cophenetic correlation were larger than for the correlation phenogram and, generally, the results of the distance phenogram agreed more closely with results of other analyses. A matrice of correlation among characters then was computed, and the first three principal components extracted.

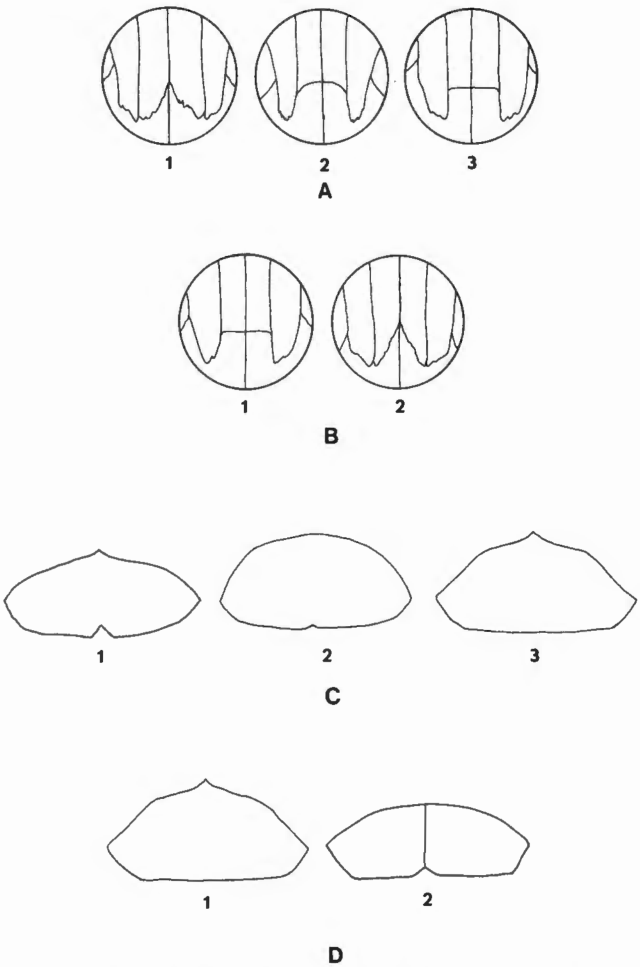

FIG. 2.—Semidiagrammatic illustration of classes used in scoring qualitative cranial characters. A, shape of posterior margin of nasals (1, emarginate; 2, rounded; 3, truncate); B, length of premaxillary bones (1, longer than nasals; 2, equal to nasals); C, posterior margin of interparietal bone (1, notched; 2, slightly notched; 3, unnotched); D, condition of interparietal bone (1, undivided; 2, divided).

Both two-dimensional and three-dimensional projections of the OTUs onto the first three principal components were made; three-dimensional projections were drawn using a Benson-Lehner incremental plotter (Rohlf, 1968). Discussions of the theory underlying these tests were given by Sokal and Sneath (1963), Schnell (1970:42-44), and Atchley (1970:206-212). Choate (1970), Rising (1970), and Genoways and Jones (1971) have used these techniques in studies similar to mine.

Discriminant function analyses were performed using the MULDIS subroutine of the NT-SYS system. This program used variance-covariance mathematics to differentially weight characters relative to their within-group and between-groups variation. Only two reference samples were used for all discriminant analyses in this paper; these two reference samples were either samples of two species in which I was studying character differences or samples geographically removed from zones suspected of hybridization or intergradation with which a sample from the intermediate geographical area was compared. A discriminant multiplier was calculated using the reference samples for each character, and this was multiplied by the value of its respective character; all such values were summed for each individual to yield its discriminant score. Where hybridization or intergradation was suspected, the discriminant scores were plotted on a frequency histogram to compare individuals of the two reference samples and to compare the test sample from the intermediate geographical area. A good discussion of discriminant functions was given by Jolicoeur (1959). Lawrence and Bossert (1969), Birney (1970), and Genoways and Choate (1972) have used this test in studying other mammalian groups.

Ratio diagrams were prepared using a program written for Olivetti Underwood Programma 101 by Sydney Anderson. Ratio diagrams are graphic methods of analysis first used by Simpson (1941) and discussed later by Simpson *et al.* (1960). Musser (1969*a*, 1969*b*, 1970) has used this technique in several recent papers dealing with systematic problems of mammals. Other less frequently used tests such as Student's *t*-test and Wilcoxon two-sample test are based upon procedures outlined by Sokal and Rohlf (1969); all statistical terminology is also based upon that used by Sokal and Rohlf.

In my analysis of evolutionary relationships, a Prim Network was computed. The Prim Network (Prim, 1957) is an expression of the phenetic relationships of the species based upon all characters considered (characters not weighted). The patristic difference (the length of the line connecting two species and the corresponding numerical value) represents the proportional overall difference that separates the species. Angles between cladistic events are arbitrary. This network also provides a framework for an inference of primitive character states and ancestral forms. I had planned to also produce a Wagner Diagram, but this was not done because a satisfactory method could not be found for weighting the many binary and coded characters used in my analyses that do not vary within species. Theories underlying these techniques and their application are discussed in detail by Ferris (1966, 1967, 1970), Kluge (1969), and Kluge and Ferris (1969); Lawlor (1971) has recently used these analyses in studying members of the genus *Peromyscus* from the islands in the Gulf of California. My analysis was carried out using a computer program supplied by J. S. Ferris to S. R. Edwards.

I am deeply indebted to the following institutions and curators who made material in their care available to me for study. Abbreviations preceding the names of institutions are used in the accounts beyond to identify the source of specimens.

AMNH—American Museum of Natural History, New York City (Richard G. Van Gelder and Sydney Anderson)

ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia (Robert R. Grant, Jr.)

BMNH—British Museum (Natural History), London (J. E. Hill)
CAS—California Academy of Sciences, San Francisco (Robert T. Orr)
ENCB—Escuela Nacional de Ciencias Biológicas, México, D. F. (Ticul Alvarez)
FMNH—Field Museum of Natural History, Chicago (Joseph C. Moore)
KU—Museum of Natural History, The University of Kansas, Lawrence (J. Knox Jones, Jr.)
LACM—Los Angeles County Museum, Los Angeles (Donald R. Patten)
LSU—Museum of Natural Science, Louisiana State University, Baton Rouge (George H. Lowery, Jr.)
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge (Barbara Lawrence)
MSU—The Museum, Michigan State University, East Lansing (Rollin H. Baker)
MVZ—Museum of Vertebrate Zoology, The University of California, Berkeley (William Z. Lidicker, Jr., and Seth B. Benson)
MWU—Department of Biology, Midwestern University, Wichita Falls, Texas (Walter W. Dalquest)
ROM—Royal Ontario Museum, Toronto (Randolph L. Peterson and James R. Tamsitt)
SDNHM—San Diego Natural History Museum, San Diego (Joseph R. Jehl, Jr.)
TCWC—Texas Cooperative Wildlife Collection, Texas A&M University, College Station (Dilford C. Carter and William B. Davis)
TNHC—Texas Natural History Collection, The University of Texas, Austin (W. W. Newcomb)
TTU—Texas Tech University, Lubbock (Robert L. Packard and Robert J. Baker)
UA—University of Arizona, Tucson (E. Lendell Cockrum)
UCLA—University of California, Los Angeles, including the Donald R. Dickey Collection (Thomas R. Howell)
UMMZ—Museum of Zoology, The University of Michigan, Ann Arbor (Emmet T. Hooper and William H. Burt)
UNAM—Instituto de Biología, Universidad Nacional Autonoma de México, México, D. F. (Bernardo Villa-R.)
UNM—Museum of Southwestern Biology, University of New Mexico, Albuquerque (James S. Findley)
USNM—United States National Museum, including the Biological Surveys Collection, Washington, D. C. (Charles O. Handley, Jr., Henry W. Setzer, and John L. Paradiso)
WBC—Wayland Baptist College, Plainview, Texas (J. Hoyt Bowers)
YPM—The Peabody Museum of Natural History, Yale University, New Haven (Charles G. Sibley)

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Research and Development Command. Photographic and other supplies were purchased with funds supplied by Research Awards Committee of the Kansas Academy of Science and the Division of Biological Sciences, The University of Kansas. Computer time allotted to me by the Division of Biological Sciences enabled use of the GE 635 computer at The University of Kansas.

I am especially grateful to Dr. J. Knox Jones, Jr., who supervised my research and critically reviewed this manuscript. Dr. George W. Byers and Dr. Sydney Anderson also reviewed the manuscript and made many helpful suggestions. T. H. Swearingen and B. Siler prepared the cranial and dental drawings. Some drawings and measurements of special structures were made with the aid of a Wild Heerbrugg Stereomicroscope fitted with a drawing tube, kindly made available to me by Dr. F. B. Cross. Dr. Richard F. Johnston placed at my disposal a Bausch and Lomb Spectronic 505 recording spectrophotometer. The section on karyology could not have been completed without the help of Dr. Robert J. Baker, who gave freely his supplies, equipment, and time, and Dr. James L. Patton and Dr. Alfred L. Gardner. Mr. Eustorgio Méndez of the Gorgas Memorial Laboratory supplied live specimens of *Liomys adspersus* and *Heteromys desmarestianus* from Panamá. I would like to extend my gratitude to the many people who collected material used in this report with particular thanks to Percy L. Clifton and J. R. Alcorn, who made large and significant collections for The University of Kansas. Dr. Craig C. Black made available the holotype of *Liomys centralis* and tendered his opinion on the status of that fossil species.

My early graduate training was done under the guidance of Dr. E. R. Hall. Several of my colleagues at The University of Kansas, especially Drs. Elmer C. Birney, Jerry R. Choate, Carleton J. Phillips, and James D. Smith were helpful in giving technical assistance and willingly engaged in stimulating discussions pertinent to my research.

Special thanks are extended to the following specialists who identified ectoparasites of *Liomys* and *Heteromys* and checked the lists of ectoparasites in Appendix II: Dr. K. C. Emerson (Anoplura), Dr. J. Kethley (Cheyletidae), Dr. C. E. Yunker (Dermanyssidae), Drs. G. M. Kohls and E. K. Jones (Ixodides), Dr. R. W. Strandtmann (Laelapidae), Dr. B. McDaniel (Listrophoridae), Dr. R. Traub (Siphonaptera), and Dr. R. B. Loomis (Trombiculidae).

Finally, I especially acknowledge my wife, Joyce, who prepared many of the illustrations, typed the drafts of this manuscript, and provided the moral support necessary to see this project through to its completion.

The systematic accounts are introduced by remarks on the distribution, diagnosis, comparisons with other species, and general ecology of the species without reference to infraspecific variation. These sections are followed by the analysis of geographic variation, both univariate and multivariate. For the statistical analyses, it was necessary to group specimens from several localities in order to have large enough samples for testing. In grouping localities, I attempted to keep the included geographic area as small as possible, not to cross any major physiographic boundaries, and not to cross previously recognized taxonomic boundaries. The localities grouped for each sample are listed in the appropriate species account in an abbreviated form; precise localities can be found in lists of specimens examined. Following the analyses of geographic variation are the taxonomic conclusions based on these analyses.

The synonymies in the subspecific accounts are arranged with the original description first, followed by the first use of the presently employed name combination and, finally, any junior synonyms. Although the International Code of Zoological Nomenclature (Article 51b) prohibits the use of a comma between a scientific name and the name of a user subsequent to the original author, I have done so in my synonymies because it has been, and still is, a common practice in the mammalogical literature. Following the synonymies are a brief description of the holotype of the subspecies, distribution of the subspecies, and comparisons with other subspecies within the species. The remarks section contains comments on relationship and intergradation with other subspecies of the species, on relationship with sympatric species, and on infrasubspecies variation. In the lists of specimens examined the countries and states are listed alphabetically, and within each political unit the towns or physiographic features are listed alphabetically. If more than one locality is listed with reference to a particular place-name, the localities are arranged with the most northwesterly first and the most southeasterly last. A gazetteer is provided in Appendix I. Specimens examined are followed by a list of additional records from the literature and a list of marginal records. The marginal records are plotted on the distribution maps for the appropriate species (excepting those in italics, which have not been plotted because undue crowding of symbols would have resulted). The first marginal record listed is the northernmost for the subspecies, and subsequent localities are listed in a clockwise manner from this starting point in the fashion employed by Hall and Kelson (1959).

At this point it seems appropriate to define my ideas about two concepts—those of the species and the subspecies—used extensively in this paper. The "biological" species concept has been followed insofar as it was possible to do so. This concept may be simply stated that species are "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1966). In the genus *Liomys*, I have found no difficulty in applying this concept because no individual that could be identified as a hybrid between species was found. My concept of a mammalian subspecies was most succinctly stated by Lidicker (1962:169, see also 1960:161-63) as follows: "A subspecies is a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographical area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies." This is an appealing concept because it views a subspecies as a population that has made initial steps toward speciation (although most do not complete the process) and applies an evolutionary philosophy to infraspecific variation rather than viewing it solely as geographic variation.

NONGEOGRAPHIC VARIATION

Four types of nongeographic variation—variation with age, secondary sexual variation, individual variation, and seasonal and maturational molts—are discussed in the following section. Appreciation of these types of variation is necessary in studies of the kind presented herein, because they must be taken into account and their effects thus minimized or eliminated when geographic variation is considered.

Variation with Age

When variation with age is present in a taxon, it is necessary in studies of geographic variation of the taxon to identify those age categories that represent "adults" in that the individuals have stopped or nearly stopped growing. Specimens from selected populations of three species of *Liomys* (*irroratus*, *pictus*, and *salvini)* were assigned to one of five age categories and external and cranial measurements were recorded for all individuals in order to determine what mensural variation with age occurred in these populations. The age categories are defined below, listed in sequence of increasing age. Numbers given after dental characters refer to toothrows of *Liomys salvini* shown in Fig. 3, which illustrate the characters, and toothrows illustrated by Reeder (1953:62) for *Liomys pictus.*

I—M3 not fully erupted; deciduous premolars present (I); braincase domed; rostrum proportionally short; cranial bones only loosely articulated; juvenile pelage.

II—M3 fully erupted; deciduous premolars present (II); braincase becoming flattened; cranial bones firmly articulated but all sutures plainly evident; juvenile or adult pelage (many individuals molting from juvenile pelage).

III—Permanent premolar present but little worn; M1 revealing little evidence of wear, the median valley still completely separating the anterior and posterior lophs (III and 1-3 of Reeder); most sutures still evident; presphenoid-basioccipital suture usually open, but closed in a few individuals; temporal ridges only weakly defined especially in the parietal region; adult pelage.

IV—M1 heavily worn so that only a dentine lake surrounded by a rim of enamel remaining (some individuals of *L. salvini* were judged to be adults when M1 evinced enough wear so that the anterior and posterior lophs joined at least at one end, if the other criteria were met) (IV and 4-5 of Reeder); presphenoid-basioccipital suture closed; sutures between nasals and frontals becoming obscured as are those between interparietal and parietals; temporal ridges well defined, even in the parietal region.

V—All molars so heavily worn that no enamel pattern remains on their occlusal surface, excepting possibly a small enamel island on M3 (V and 7-10 of Reeder).

Each of the 13 external and cranial characters were tested separately for males and females with single classification anova to determine if any of the means of the age categories were significantly different at $P<.05$. If the means were found to be significantly different, the simultaneous sums of squares testing procedure

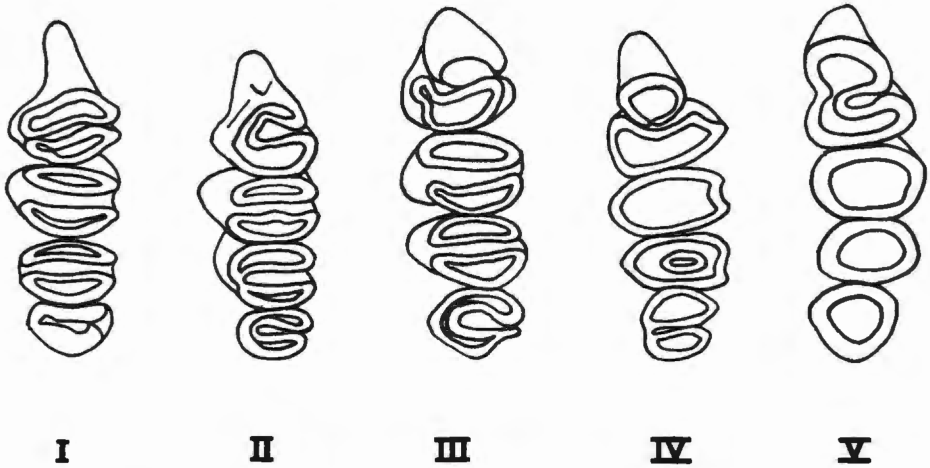


FIG. 3.—Left maxillary toothrows of *Liomys salvini* illustrating wear patterns for the five age categories. See text for description of age categories.

was used to find maximally nonsignificant subsets. The results of these tests are discussed below and shown in Table 1.

Liomys irroratus.—Length of maxillary toothrow, depth of braincase, interparietal width, and interparietal length for both males and females were the only four characters tested that were found to have no significant difference between the means of all age categories. Nonoverlapping subsets of I, II-III, and IV-V were exhibited by four characters for both sexes (total length, length of tail, length of nasals, and length of rostrum for males and total length, greatest length of skull, length of nasals, and length of rostrum for females) of the remaining nine. Age category I formed a subset that differed significantly from the other four categories in length of hind foot of females. In greatest length of skull for males, nonoverlapping subsets of I-II, III, and IV-V were formed and subsets I, II-III-IV, and V were formed by age categories for interorbital constriction of females. The remaining characters (length of hind foot, zygomatic breadth, interorbital constriction, and mastoid breadth for males and length of tail, zygomatic breadth, and mastoid breadth for females) displayed more complex patterns of overlapping subsets, but in all for the females, and one for the males (mastoid breadth) category I formed a subset distinct from the other four categories. In only one character—interorbital breadth of females—of all those tested was a significant difference found between categories IV and V. In only four instances (length of hind foot of females and depth of braincase, interparietal width, and interparietal length of males) were the means of groups IV and V not found to be the largest. Group I was found to have the smallest mean in all characters except interparietal width of males and interparietal length of females, and in both the analysis of variance was nonsignificant.

Liomys pictus.—Males were found to have no significant difference between the means of the age categories in two characters (interparietal width and interparietal length) and females in only one character (length of maxillary toothrow). Nonoverlapping subsets of I, II-III, and IV-V were found in five characters for males (total length, length of tail, greatest length of skull, length of nasals, and length of rostrum) and two characters for females (greatest length of skull and length of rostrum). Two other patterns of nonoverlapping subsets were illustrated in this species, I-II-III and IV-V for zygomatic breadth of males and interorbital constriction of females and I-II, III, and IV-V for zygomatic breadth of females. The remaining characters (length of hind foot, interorbital constriction, mastoid breadth, length of maxillary toothrow, and depth of braincase for males and total length, length of tail, length of hind foot, zygomatic breadth, length of nasals, depth of braincase, interparietal width, and interparietal length for females) showed complex patterns of overlapping subsets, but in two of the characters for females (length of nasals and interparietal width) category I was separate from the other four. In no case was category IV found to be significantly different from V. Either category IV or V had the largest mean for all characters studied and for all measurements category I had the smallest mean.

Liomys salvini.—In one measurement for males (length of maxillary toothrow) and three for females (length of maxillary toothrow, interparietal width, and interparietal length) no significant difference was found between the various age categories. Nonoverlapping subsets of I, II, and III-IV-V were shown in total length for females. Greatest length of skull and zygomatic breadth for males have subsets of I, II-III, and IV-V and age categories for depth of braincase for males were divided into two subsets (I-II-III and IV-V). Two measurements for males (length of nasals and length of rostrum) and three for females (greatest length of skull, length of nasals, and length of rostrum) have nonoverlapping subsets of I, II, III, and IV-V. However, the majority of measurements for *Liomys salvini* show a complex pattern of overlapping subsets. Seven measurements for males (total length, length of tail, length of hind foot, interorbital constriction, mastoid breadth, interparietal width, and interparietal length) and six for females (length of tail, length of hind foot, zygomatic breadth, interorbital constriction, mastoid breadth, and depth of braincase) exhibit overlapping subsets. In three characters with overlapping subsets for both males (total length, length of tail, and mastoid breadth) and females (length of tail, zygomatic breadth, and mastoid breadth), category I formed a subset that was distinct from the remaining categories. In no measurement was age category IV found to be significantly different from V. In all cases either IV or V had the largest mean and category I had the smallest mean.

Conclusions.—In the three species studied, age categories IV and V represent the largest individuals and individuals of the two groups are inseparable based on size. Specimens falling into these two categories have been used as "adults" throughout the remainder of my study and form the basis for the analysis in interspecific and intraspecific variation. For *Liomys irroratus* and *L. pictus*, the three remaining categories appear to fall into two groups—I and II-III. For *Liomys salvini* the situation is not as clear, but it would appear that the three remaining categories can best be considered as distinct from each other.

TABLE 1.—*Variation with age in external and cranial measurements of three species of* Liomys. *The three species (in the order that they appear in the table) are* Liomys irroratus *from central Jalisco,* Liomys pictus *from western Jalisco, and* Liomys salvini *from the departments of Carazo and Managua, Nicaragua. Statistics given are number, mean, two standard errors of mean, range, coefficient of variation,* F, *and* F_S. *Age classes for the males are listed first for each measurement followed by those for females; the age classes are listed in decreasing order with the largest mean first. Groups of means that were found to be significantly different at* P<.05 *were tested with the sums of squares-simultaneous testing procedure to find the nonsignificant subsets. Groups of means that were found to be not significantly different at* P<.05 *are marked ns.*

Measurements, sex, and age classes	N	Mean ± 2 SE	Range	CV	F_s / F	Results SS-STP
		Liomys irroratus				
Total length						
Male						
V	4	251.5 ± 9.00	(240.0-262.0)	3.6	41.22	
IV	18	235.1 ± 5.07	(216.0-253.0)	4.6	2.60	
III	13	219.2 ± 5.01	(202.0-231.0)	4.1		
II	7	205.1 ± 4.20	(195.0-210.0)	2.7		
I	4	184.0 ± 8.16	(174.0-194.0)	4.4		
Female						
V	8	228.6 ± 5.21	(215.0-237.0)	3.2	27.24	
IV	26	225.3 ± 3.78	(207.0-251.0)	4.3	2.53	
III	19	215.1 ± 3.75	(201.0-233.0)	3.8		
II	6	207.8 ± 4.39	(198.0-212.0)	2.6		
I	3	175.3 ± 16.71	(166.0-192.0)	8.3		
Length of tail						
Male						
V	4	127.3 ± 8.22	(118.0-138.0)	6.5	30.89	
IV	18	118.6 ± 3.26	(106.0-130.0)	5.8	2.60	
III	13	111.2 ± 2.74	(100.0-118.0)	4.5		
II	7	102.6 ± 3.51	(95.0-107.0)	4.5		
I	4	88.5 ± 4.80	(84.0-94.0)	5.4		
Female						
IV	26	112.6 ± 2.48	(102.0-131.0)	5.6	19.74	
V	8	112.3 ± 2.58	(105.0-116.0)	3.3	2.53	
III	19	107.1 ± 2.80	(97.0-118.0)	5.7		
II	6	104.3 ± 3.21	(97.0-107.0)	3.8		
I	3	82.3 ± 9.68	(77.0-92.0)	10.2		

TABLE 1.—*Continued.*

Length of hind foot					
Male					
V	4	29.9 ± 1.03	(28.5-31.0)	3.5	4.13
III	14	29.4 ± 0.35	(28.0-30.0)	2.2	2.60
IV	17	29.0 ± 0.54	(26.0-30.5)	3.8	
II	7	28.9 ± 0.52	(28.0-30.0)	2.4	
I	4	27.6 ± 0.75	(26.5-28.0)	2.7	
Female					
II	6	28.8 ± 0.33	(28.0-29.0)	1.4	7.91
III	19	28.6 ± 0.28	(27.0-29.5)	2.2	2.52
IV	28	28.2 ± 0.32	(27.0-30.0)	3.0	
V	8	28.2 ± 0.53	(27.0-29.0)	2.7	
I	3	26.0 ± 2.08	(24.5-28.0)	6.9	
Greatest length of skull					
Male					
V	3	33.2 ± 0.92	(32.6-34.1)	2.4	31.34
IV	18	31.9 ± 0.51	(30.4-34.1)	3.4	2.60
III	14	30.7 ± 0.23	(29.9-31.3)	1.4	
II	7	29.3 ± 0.74	(27.8-30.3)	3.4	
I	4	27.8 ± 0.51	(27.1-28.3)	1.8	
Female					
V	8	31.6 ± 0.51	(30.8-33.0)	2.3	54.08
IV	25	31.4 ± 0.23	(30.3-32.6)	1.9	2.53
III	19	30.4 ± 0.29	(29.0-31.3)	2.1	
II	6	29.7 ± 0.28	(29.2-30.1)	1.2	
I	3	26.2 ± 1.30	(25.5-27.5)	4.3	
Zygomatic breadth					
Male					
V	3	16.3 ± 0.24	(16.1-16.5)	1.3	20.39
IV	16	15.4 ± 0.29	(14.8-16.6)	3.8	2.62
III	14	14.8 ± 0.14	(14.3-15.1)	1.8	
II	7	14.5 ± 0.26	(14.0-15.0)	2.4	
I	3	13.7 ± 0.29	(13.5-14.0)	1.8	
Female					
V	7	15.5 ± 0.21	(15.0-15.9)	1.8	17.79
IV	20	15.2 ± 0.21	(14.6-16.3)	3.1	2.56
II	6	14.8 ± 0.12	(14.6-15.0)	1.0	
III	17	14.6 ± 0.17	(13.9-15.2)	2.4	
I	3	13.6 ± 0.37	(13.4-14.0)	2.4	

TABLE 1.—*Continued.*

Interorbital constriction					
Male					
V	4	8.3 ± 0.10	(8.2-8.4)	1.2	10.11
IV	18	7.9 ± 0.18	(7.2-8.7)	4.8	2.59
III	14	7.6 ± 0.86	(7.3-7.9)	2.1	
II	7	7.6 ± 0.27	(7.2-8.2)	4.8	
I	4	7.1 ± 0.20	(6.8-7.2)	2.8	
Female					
V	8	7.9 ± 0.16	(7.7-8.3)	2.8	13.15
IV	27	7.6 ± 0.98	(7.2-8.1)	3.4	2.52
III	19	7.5 ± 0.86	(7.2-7.8)	2.5	
II	6	7.5 ± 0.13	(7.3-7.7)	2.1	
I	3	6.9 ± 0.18	(6.7-7.0)	2.2	
Mastoid breadth					
Male					
V	3	14.7 ± 0.29	(14.5-15.0)	1.7	9.66
IV	18	14.5 ± 0.20	(13.8-15.4)	3.0	2.62
II	6	14.2 ± 0.22	(13.8-14.5)	1.9	
III	14	14.1 ± 0.95	(13.8-14.4)	1.3	
I	3	13.4 ± 0.46	(13.0-13.8)	3.0	
Female					
V	8	14.4 ± 0.19	(13.8-14.6)	1.9	22.67
IV	25	14.3 ± 0.93	(13.8-14.7)	1.6	2.53
II	6	14.1 ± 0.99	(13.9-14.2)	0.9	
III	19	14.0 ± 0.11	(13.7-14.5)	1.6	
I	3	13.1 ± 0.41	(12.7-13.4)	2.7	
Length of nasals					
Male					
V	4	12.9 ± 0.35	(12.5-13.3)	2.7	31.26
IV	18	12.4 ± 0.32	(11.4-13.4)	5.5	2.59
III	14	11.4 ± 0.23	(10.9-12.3)	3.8	
II	7	10.8 ± 0.34	(10.3-11.6)	4.1	
I	4	9.6 ± 0.57	(8.8-10.0)	5.9	
Female					
V	8	12.6 ± 0.39	(11.6-13.2)	4.4	33.00
IV	28	12.1 ± 0.22	(11.0-13.5)	4.9	2.52
III	19	11.5 ± 0.18	(10.5-12.4)	3.4	
II	6	11.1 ± 0.33	(10.8-11.9)	3.7	
I	3	9.1 ± 0.55	(8.7-9.6)	5.2	

TABLE 1.—*Continued.*

Length of rostrum						
Male						
V	4	14.7 ± 0.34	(14.5-15.2)	2.3	38.73	
IV	18	14.1 ± 0.30	(13.2-15.4)	4.5	2.59	
III	14	13.1 ± 0.16	(12.6-13.5)	2.3		
II	7	12.5 ± 0.33	(11.8-13.0)	3.5		
I	4	11.5 ± 0.38	(11.0-11.9)	3.3		
Female						
V	8	14.0 ± 0.23	(13.7-14.7)	2.3	48.11	
IV	28	13.7 ± 0.15	(13.0-14.9)	2.9	2.52	
III	19	13.1 ± 0.19	(12.3-13.7)	3.1		
II	6	12.7 ± 0.15	(12.4-12.9)	1.5		
I	3	10.7 ± 1.11	(10.0-11.8)	9.0		
Length of maxillary toothrow						
Male						
IV	18	5.1 ± 0.08	(4.8-5.4)	3.1	2.41	ns
III	14	5.1 ± 0.07	(4.8-5.3)	2.7		
V	4	5.0 ± 0.14	(4.9-5.2)	2.8	3.29	
Female						
IV	28	5.1 ± 0.06	(4.8-5.4)	3.3	0.58	ns
V	8	5.0 ± 0.22	(4.4-5.2)	6.0	3.18	
III	19	5.0 ± 0.08	(4.8-5.4)	3.4		
Depth of braincase						
Male						
III	14	8.8 ± 0.16	(8.4-9.4)	3.4	1.89	ns
V	2	8.7	(8.7)		2.63	
IV	18	8.7 ± 0.13	(8.2-9.2)	3.2		
II	5	8.6 ± 0.20	(8.4-9.0)	2.5		
I	3	8.3 ± 0.31	(8.1-8.6)	3.2		
Female						
V	8	8.7 ± 0.09	(8.5-8.8)	1.4	1.90	ns
IV	25	8.6 ± 0.08	(8.2-9.0)	2.3	2.54	
III	19	8.6 ± 0.06	(8.3-8.8)	1.6		
II	6	8.6 ± 0.14	(8.5-9.0)	2.0		
I	2	8.4 ± 0.10	(8.3-8.4)	0.8		
Interparietal width						
Male						
III	14	8.8 ± 0.24	(7.5-9.3)	5.1	0.51	ns
IV	18	8.7 ± 0.21	(7.9-9.4)	5.1	2.61	
II	6	8.6 ± 0.35	(7.9-9.0)	5.1		
I	4	8.6 ± 0.26	(8.2-8.8)	3.1		
V	3	8.5 ± 0.44	(8.2-8.9)	4.5		

TABLE 1.—*Continued.*

Female						
V	8	8.7 ± 0.20	(8.2-9.0)	3.3	0.77	ns
III	19	8.5 ± 0.20	(7.9-9.3)	5.0	2.54	
II	6	8.5 ± 0.35	(7.9-9.0)	5.0		
IV	26	8.4 ± 0.16	(7.8-9.5)	4.8		
I	3	8.3 ± 0.20	(8.2-8.5)	2.1		
Interparietal length						
Male						
III	14	3.7 ± 0.12	(3.4-4.0)	5.8	1.38	ns
V	3	3.6 ± 0.44	(3.2-3.9)	10.4	2.61	
IV	18	3.6 ± 0.12	(3.0-4.1)	6.8		
II	6	3.5 ± 0.15	(3.2-3.7)	5.4		
I	4	3.5 ± 0.29	(3.2-3.9)	8.1		
Female						
V	8	3.7 ± 0.16	(3.3-4.0)	6.0	0.53	ns
III	19	3.7 ± 0.15	(3.0-4.3)	9.0	2.54	
IV	26	3.6 ± 0.12	(2.9-4.1)	8.2		
I	3	3.6 ± 0.50	(3.3-4.1)	12.1		
II	6	3.5 ± 0.33	(3.0-4.1)	11.6		
		Liomys pictus				
Total length						
Male						
V	2	253.5 ± 9.00	(249.0-258.0)	2.5	32.61	
IV	33	240.3 ± 4.21	(218.0-264.0)	5.0	2.56	
III	16	224.5 ± 4.22	(208.0-239.0)	3.8		
II	10	214.2 ± 5.56	(199.0-226.0)	4.1		
I	4	185.0 ± 15.43	(165.0-201.0)	8.3		
Female						
V	2	232.0 ± 18.00	(223.0-241.0)	5.5	15.29	
IV	25	229.5 ± 3.87	(212.0-248.0)	4.2	2.56	
III	19	216.6 ± 4.61	(192.0-230.0)	4.6		
II	5	207.0 ± 8.85	(196.0-220.0)	4.8		
I	2	183.3 ± 23.50	(171.5-195.0)	9.1		
Length of tail						
Male						
V	2	131.5 ± 1.00	(131.0-132.0)	0.5	22.08	
IV	33	123.0 ± 2.88	(105.0-138.0)	6.7	2.56	
III	16	115.0 ± 2.85	(109.0-127.0)	5.0		
II	10	108.7 ± 4.41	(98.0-117.0)	6.4		
I	4	92.1 ± 7.58	(82.5-101.0)	8.2		

TABLE 1.—*Continued.*

Female					
V	2	121.5 ± 9.00	(117.0-126.0)	5.2	9.20
IV	25	118.2 ± 2.30	(108.0-128.0)	4.9	2.56
III	19	111.6 ± 4.06	(91.0-125.0)	7.9	
II	5	104.4 ± 7.50	(94.0-116.0)	8.0	
I	2	93.5 ± 9.00	(89.0- 98.0)	6.8	
Length of hind foot					
Male					
V	4	29.1 ± 1.31	(28.0-31.0)	4.5	3.84
IV	36	28.8 ± 0.37	(26.0-31.0)	3.9	2.56
II	11	28.4 ± 0.47	(27.0-29.5)	2.7	
III	17	27.9 ± 0.42	(26.0-29.0)	3.1	
I	4	27.5 ± 1.35	(25.5-28.5)	4.9	
Female					
IV	27	28.7 ± 0.45	(27.0-31.0)	4.1	8.02
V	7	27.9 ± 0.81	(26.0-29.0)	3.8	2.54
III	20	27.7 ± 4.00	(26.0-29.5)	3.2	
II	5	26.7 ± 1.41	(25.0-28.0)	5.9	
I	2	25.0 ± 2.00	(24.0-26.0)	5.7	
Greatest length of skull					
Male					
V	4	32.7 ± 0.67	(32.1-33.4)	2.0	54.04
IV	35	32.2 ± 0.26	(30.8-34.1)	2.4	2.51
III	19	30.4 ± 0.37	(28.5-31.8)	2.6	
II	10	29.5 ± 0.56	(28.3-30.8)	3.0	
I	4	27.7 ± 0.97	(26.6-28.7)	3.5	
Female					
V	6	31.6 ± 0.74	(30.2-32.8)	2.9	27.76
IV	28	31.6 ± 0.28	(30.1-33.0)	2.3	2.54
III	19	30.1 ± 0.41	(27.7-31.3)	2.9	
II	5	29.6 ± 0.73	(28.5-30.6)	2.8	
I	2	26.5 ± 2.00	(25.5-27.5)	5.3	
Zygomatic breadth					
Male					
V	3	15.1 ± 0.53	(14.6-15.4)	3.1	15.61
IV	27	15.0 ± 0.15	(14.1-15.9)	2.6	2.54
III	19	14.4 ± 0.21	(13.7-15.3)	3.2	
II	10	14.0 ± 0.23	(13.4-14.7)	2.6	
I	2	13.7 ± 0.20	(13.6-13.8)	1.0	

TABLE 1.—*Continued.*

Female						
V	5	14.7 ± 0.36	(14.1-15.0)	2.7	19.08	
IV	26	14.6 ± 0.13	(14.1-15.2)	2.3	2.56	
III	17	14.2 ± 0.14	(13.5-14.8)	2.1		
II	5	13.6 ± 0.33	(13.3-14.2)	2.7		
I	2	13.2 ± 0.30	(13.0-13.3)	1.6		
Interorbital constriction						
Male						
IV	36	7.8 ± 0.11	(7.1-8.7)	4.2	9.27	
V	4	7.7 ± 0.54	(7.1-8.4)	7.0	2.50	
III	20	7.5 ± 0.11	(7.1-8.0)	3.4		
II	12	7.2 ± 0.24	(6.2-7.8)	5.7		
I	4	7.1 ± 0.08	(7.0-7.2)	1.1		
Female						
V	7	7.9 ± 0.19	(7.5-8.3)	3.2	11.95	
IV	28	7.6 ± 0.12	(7.1-8.6)	4.1	2.54	
III	20	7.3 ± 0.09	(6.9-7.6)	2.7		
II	5	7.3 ± 0.08	(7.2-7.4)	1.2		
I	2	6.8 ± 0.10	(6.7-6.8)	1.0		
Mastoid breadth						
Male						
IV	35	14.3 ± 0.13	(13.6-15.0)	2.6	10.60	
V	4	14.2 ± 0.37	(13.7-14.6)	2.6	2.50	
III	20	14.1 ± 0.14	(13.3-14.7)	2.2		
II	12	13.7 ± 0.21	(13.2-14.4)	2.7		
I	4	13.4 ± 0.31	(13.0-13.7)	2.3		
Female						
IV	28	14.2 ± 0.13	(13.6-14.8)	2.3	7.74	
V	7	14.0 ± 0.17	(13.5-14.2)	1.6	2.54	
III	20	13.9 ± 0.17	(13.0-14.5)	2.7		
II	5	13.5 ± 0.58	(12.8-14.5)	4.8		
I	2	13.0 ± 0.10	(12.9-13.0)	0.5		
Length of nasals						
Male						
V	4	13.3 ± 0.48	(12.6-13.7)	3.6	52.62	
IV	36	13.0 ± 0.19	(11.7-14.3)	4.5	2.51	
III	20	11.9 ± 0.21	(10.6-12.6)	3.9		
II	12	11.5 ± 0.17	(11.0-12.1)	2.6		
I	4	10.2 ± 0.33	(9.7-10.4)	3.3		

TABLE 1.—*Continued.*

Female						
IV	28	12.7 ± 0.23	(11.1-13.9)	4.7	21.19	
V	6	12.7 ± 0.53	(11.9-13.3)	5.1	2.54	
III	19	11.8 ± 0.22	(11.0-12.8)	4.0		
II	5	11.3 ± 0.64	(10.3-12.3)	6.3		
I	2	9.5 ± 1.50	(8.7-10.2)	11.2		
Length of rostrum						
Male						
V	4	14.3 ± 0.05	(14.3-14.4)	0.3	50.31	
IV	34	14.2 ± 0.18	(13.1-15.5)	3.6	2.51	
III	19	13.1 ± 0.25	(11.8-14.1)	4.1		
II	11	12.5 ± 0.31	(11.8-13.5)	4.1		
I	4	11.3 ± 0.51	(10.7-11.9)	4.5		
Female						
V	6	13.9 ± 0.47	(13.0-14.6)	4.1	23.73	
IV	26	13.8 ± 0.20	(13.0-14.8)	3.6	2.55	
III	18	13.0 ± 0.22	(12.2-13.6)	3.7		
II	4	12.7 ± 0.41	(12.1-13.1)	3.3		
I	2	10.9 ± 0.80	(10.5-11.3)	5.2		
Length of maxillary toothrow						
Male						
V	4	5.1 ± 0.18	(4.9-5.3)	3.6	3.55	
IV	32	4.9 ± 0.06	(4.6-5.4)	3.5	3.18	
III	19	4.9 ± 0.08	(4.5-5.1)	3.7		
Female						
V	7	4.9 ± 0.19	(4.4-5.1)	5.2	2.16	ns
IV	28	4.9 ± 0.07	(4.5-5.2)	3.9	3.18	
III	19	4.8 ± 0.08	(4.4-5.2)	3.6		
Depth of braincase						
Male						
V	4	8.5 ± 0.41	(8.1-8.9)	4.8	6.09	
IV	35	8.3 ± 0.07	(7.8-8.7)	2.4	2.50	
III	19	8.2 ± 0.10	(7.8-8.7)	2.7		
II	12	8.0 ± 0.11	(7.7-8.4)	2.3		
I	4	8.0 ± 0.32	(7.5-8.2)	4.0		
Female						
V	6	8.3 ± 0.26	(8.0-8.8)	3.8	3.85	
II	5	8.2 ± 0.16	(8.0-8.5)	2.2	2.55	
IV	27	8.2 ± 0.09	(7.7-8.6)	2.8		
III	19	8.1 ± 0.86	(7.9-8.5)	2.3		
I	2	7.6 ± 0.80	(7.2-8.0)	7.4		

TABLE 1.—*Continued.*

Interparietal width						
Male						
V	4	9.0 ± 0.22	(8.7-9.2)	2.5	1.64	ns
IV	35	8.9 ± 0.14	(7.9-9.7)	4.6	2.50	
III	20	8.7 ± 0.16	(8.2-9.4)	4.0		
II	12	8.6 ± 0.20	(8.0-9.1)	3.9		
I	4	8.6 ± 0.44	(8.1-9.1)	5.2		
Female						
V	7	8.9 ± 0.39	(8.0-9.5)	5.8	3.61	
IV	28	8.8 ± 0.17	(7.9-9.5)	5.2	2.54	
II	5	8.5 ± 0.53	(7.8-9.2)	7.0		
III	20	8.4 ± 0.22	(7.6-9.5)	5.9		
I	2	8.1 ± 0.10	(8.0-8.1)	0.9		
Interparietal length						
Male						
V	4	4.7 ± 0.22	(4.5-5.0)	4.7	1.97	ns
IV	34	4.5 ± 0.10	(3.8-5.2)	6.7	2.51	
II	12	4.5 ± 0.19	(4.0-5.0)	7.2		
III	20	4.4 ± 0.11	(4.0-5.0)	5.6		
I	4	4.2 ± 0.50	(3.5-4.7)	12.0		
Female						
V	7	4.7 ± 0.26	(4.3-5.1)	7.3	8.12	
IV	28	4.4 ± 0.96	(4.0-4.9)	5.7	2.54	
II	5	4.3 ± 0.29	(3.8-4.7)	7.6		
III	20	4.3 ± 0.15	(3.7-5.0)	8.0		
I	2	3.5 ± 0.10	(3.4-3.5)	2.0		
Liomys salvini						
Total length						
Male						
IV	9	225.8 ± 6.70	(213.0-240.0)	4.5	23.06	
V	4	224.3 ± 10.44	(213.0-235.0)	4.7	2.65	
III	14	204.6 ± 8.12	(178.0-230.0)	7.4		
II	8	194.5 ± 9.69	(172.0-217.0)	7.0		
I	4	153.8 ± 15.46	(132.0-167.0)	10.1		
Female						
IV	11	210.0 ± 5.89	(196.0-227.0)	4.7	21.18	
V	5	207.2 ± 0.40	(207.0-208.0)	0.2	2.56	
III	26	203.1 ± 5.71	(182.0-241.0)	7.2		
II	12	188.5 ± 4.19	(178.0-200.0)	3.8		
I	3	145.7 ± 18.52	(129.0-161.0)	11.0		

TABLE 1.—*Continued.*

Length of tail					
Male					
V	4	115.5 ± 3.32	(113.0-120.0)	2.9	13.99
IV	9	111.6 ± 5.65	(94.0-121.0)	7.6	2.65
III	14	104.0 ± 5.05	(84.0-123.0)	9.1	
II	8	97.6 ± 6.41	(81.0-112.0)	9.3	
I	4	75.3 ± 12.28	(58.0-87.0)	16.3	
Female					
IV	11	108.5 ± 3.86	(100.0-121.0)	5.9	25.70
III	26	106.5 ± 3.14	(96.0-128.0)	7.5	2.56
V	5	104.8 ± 3.37	(101.0-111.0)	3.6	
II	12	93.8 ± 2.73	(86.0-103.0)	5.0	
I	3	71.0 ± 6.93	(65.0-77.0)	8.5	
Length of hind foot					
Male					
IV	9	27.2 ± 1.04	(25.0-30.0)	5.7	4.19
V	5	26.6 ± 0.80	(25.0-27.0)	3.4	2.63
II	10	26.0 ± 0.73	(24.0-27.0)	4.4	
III	14	25.9 ± 0.38	(25.0-28.0)	3.8	
I	5	24.8 ± 0.40	(24.0-25.0)	1.8	
Female					
IV	13	26.2 ± 0.56	(25.0-29.0)	3.9	2.83
II	14	25.9 ± 0.75	(22.0-27.0)	5.4	2.52
V	8	25.6 ± 0.75	(24.0-27.0)	4.1	
III	30	25.5 ± 0.53	(23.0-28.0)	5.7	
I	4	23.8 ± 1.26	(22.0-25.0)	5.3	
Greatest length of skull					
Male					
V	5	31.2 ± 0.54	(30.7-32.2)	1.9	58.52
IV	12	30.9 ± 0.51	(29.3-32.2)	2.9	2.61
III	14	29.2 ± 0.45	(27.5-30.1)	2.9	
II	9	28.1 ± 0.54	(27.0-29.8)	2.9	
I	5	24.8 ± 0.85	(23.5-26.0)	3.8	
Female					
V	8	30.2 ± 0.52	(28.9-31.1)	2.4	39.74
IV	11	30.1 ± 0.53	(28.7-31.3)	2.9	2.52
III	31	28.9 ± 0.29	(27.6-30.7)	2.8	
II	13	27.7 ± 0.53	(25.9-29.6)	3.4	
I	2	23.4 ± 0.30	(23.2-23.5)	0.9	

TABLE 1.—*Continued.*

Zygomatic breadth						
Male						
IV	9	14.3 ±	0.44	(13.5-15.7)	4.7	20.22
V	4	14.4 ±	0.47	(14.0-15.0)	3.3	2.73
III	8	13.5 ±	0.25	(13.2-14.2)	2.6	
II	7	13.2 ±	0.33	(12.5-13.8)	3.4	
I	4	11.9 ±	0.34	(11.5-12.2)	2.9	
Female						
V	5	14.1 ±	0.46	(13.6-14.8)	3.6	19.21
IV	10	13.8 ±	0.27	(13.0-14.5)	3.1	2.63
III	16	13.4 ±	0.14	(12.9-13.9)	2.0	
II	6	13.1 ±	0.32	(12.6-13.7)	3.0	
I	4	12.1 ±	0.43	(11.5-12.5)	3.6	
Interorbital constriction						
Male						
IV	13	6.7 ±	0.18	(6.2-7.4)	4.8	13.71
V	5	6.7 ±	0.29	(6.2-7.1)	4.9	2.59
III	14	6.5 ±	0.14	(6.0-6.9)	3.9	
II	10	6.2 ±	0.11	(5.8-6.4)	2.8	
I	5	5.9 ±	0.12	(5.7-6.0)	2.2	
Female						
V	8	6.5 ±	0.17	(6.1-6.8)	3.7	5.56
IV	15	6.5 ±	0.71	(6.2-6.8)	2.1	2.51
III	31	6.4 ±	0.08	(5.9-7.0)	3.6	
II	15	6.3 ±	0.11	(5.9-6.7)	3.4	
I	4	6.1 ±	0.06	(6.0-6.1)	1.0	
Mastoid breadth						
Male						
IV	12	13.5 ±	0.25	(12.9-13.9)	2.5	23.76
V	5	13.4 ±	0.41	(13.1-14.2)	3.4	2.60
III	14	13.0 ±	0.14	(12.5-13.3)	2.0	
II	10	12.9 ±	0.19	(12.5-13.5)	2.4	
I	5	11.9 ±	0.08	(11.8-12.0)	0.7	
Female						
V	8	13.4 ±	0.28	(12.8-13.9)	2.9	12.37
IV	15	13.3 ±	0.23	(12.7-14.2)	3.3	2.51
III	31	13.1 ±	0.12	(12.5-13.9)	2.5	
II	13	12.8 ±	0.21	(12.0-13.5)	2.9	
I	4	12.0 ±	0.33	(11.6-12.4)	2.7	

TABLE 1.—*Continued.*

Length of nasals							
Male							
V	5	12.1 ±	0.42	(11.5-12.8)	3.9	50.50	
IV	13	11.7 ±	0.24	(11.0-12.4)	3.7	2.60	
III	14	10.9 ±	0.32	(9.7-11.8)	5.5		
II	9	9.9 ±	0.31	(9.3-10.8)	4.7		
I	5	8.3 ±	0.62	(7.7-9.2)	8.2		
Female							
V	8	11.6 ±	0.37	(11.0-12.2)	4.5	41.06	
IV	13	11.4 ±	0.29	(10.4-12.2)	4.6	2.52	
III	31	10.7 ±	0.16	(9.8-11.7)	4.1		
II	15	10.1 ±	0.21	(9.5-11.1)	4.1		
I	2	8.0 ±	0.10	(7.9-8.0)	0.9		
Length of rostrum							
Male							
V	5	13.6 ±	0.46	(13.1-14.2)	3.8	59.97	
IV	13	13.2 ±	0.27	(12.4-14.3)	3.7	2.63	
III	12	12.2 ±	0.31	(11.2-13.0)	4.4		
II	8	11.4 ±	0.30	(10.8-12.1)	3.7		
I	5	9.7 ±	0.50	(9.1-10.5)	5.8		
Female							
V	8	12.9 ±	0.25	(12.4-13.3)	2.7	44.05	
IV	11	12.7 ±	0.30	(11.9-13.5)	4.0	2.53	
III	29	12.0 ±	0.14	(11.3-12.9)	3.2		
II	13	11.4 ±	0.25	(10.6-12.2)	3.9		
I	2	9.3 ±	0.50	(9.0-9.5)	3.8		
Length of maxillary toothrow							
Male							
V	5	4.5 ±	0.17	(4.2-4.7)	4.2	0.61	ns
IV	12	4.5 ±	0.10	(4.3-4.8)	3.8	3.37	
III	12	4.5 ±	0.10	(4.2-4.8)	3.9		
Female							
V	8	4.6 ±	0.11	(4.4-4.9)	3.5	0.25	ns
IV	16	4.6 ±	0.11	(4.2-5.0)	4.9	3.21	
III	24	4.6 ±	0.06	(4.2-4.9)	3.5		
Depth of braincase							
Male							
V	4	8.3 ±	0.27	(8.1-8.7)	3.3	6.88	
IV	12	8.2 ±	0.24	(7.6-9.0)	4.9	2.62	
III	13	7.8 ±	0.13	(7.5-8.2)	3.1		
II	10	7.8 ±	0.10	(7.5-8.1)	2.1		
I	5	7.7 ±	0.14	(7.5-7.9)	2.1		

TABLE 1.—*Continued.*

Female						
V	8	8.2 ± 0.20	(7.8-8.5)	3.4	5.19	
IV	13	8.1 ± 0.24	(7.5-9.2)	5.4	2.52	
III	30	8.0 ± 0.11	(7.4-8.6)	3.6		
II	12	7.8 ± 0.17	(7.3-8.5)	3.8		
I	4	7.4 ± 0.17	(7.2-7.6)	2.3		
Interparietal width						
Male						
IV	12	8.6 ± 0.27	(7.9-9.5)	5.4	3.06	
V	5	8.5 ± 0.55	(7.7-9.1)	7.2	2.60	
III	14	8.3 ± 0.18	(7.9-9.0)	4.1		
II	10	8.3 ± 0.27	(7.7-9.2)	5.1		
I	5	7.9 ± 0.20	(7.6-8.2)	2.9		
Female						
V	8	8.8 ± 0.21	(8.3-9.1)	3.4	1.26	ns
IV	14	8.7 ± 0.30	(7.6-9.8)	6.4	2.52	
II	13	8.6 ± 0.31	(7.6-9.2)	6.5		
III	30	8.4 ± 0.18	(7.2-9.4)	5.8		
I	4	8.4 ± 0.22	(8.1-8.6)	2.6		
Interparietal length						
Male						
IV	12	4.0 ± 0.15	(3.6-4.4)	6.7	4.95	
V	5	3.9 ± 0.24	(3.6-4.2)	6.9	2.60	
III	14	3.6 ± 0.20	(3.0-4.5)	10.3		
II	10	3.6 ± 0.22	(3.0-4.0)	9.8		
I	5	3.3 ± 0.28	(3.0-3.7)	9.4		
Female						
V	8	3.9 ± 0.17	(3.5-4.3)	6.2	1.51	ns
II	13	3.9 ± 0.19	(3.3-4.4)	8.8	2.52	
IV	14	3.8 ± 0.21	(3.4-4.7)	10.1		
III	30	3.7 ± 0.12	(3.0-4.4)	8.4		
I	4	3.6 ± 0.17	(3.4-3.8)	4.8		

SECONDARY SEXUAL VARIATION

Adult males (age categories IV and V) of *Liomys irroratus*, *L. pictus*, *L. salvini*, and *L. adspersus* were tested against adult females of the corresponding species using single classification anova to learn if the sexes were significantly different in size. The results of these tests are discussed below and shown in Table 2.

Liomys irroratus.—Males were found to be significantly larger than females in seven (total length, length of tail, length of hind foot, greatest length of skull, interorbital constriction, mastoid breadth, and length of rostrum) of the 13 measurements tested. In four (zygomatic breadth, length of nasals, depth of braincase, and interparietal width) of the remaining measurements, the means for males were larger than those for females; means for length of maxillary toothrow and interparietal length were the same for the two sexes.

Liomys pictus.—Males were found to be significantly larger than females in six (total length, length of tail, greatest length of skull, zygomatic breadth, length of nasals, and length of rostrum) of the 13 measurements tested. Males had larger means in four other measurements (length of hind foot, interorbital constriction, mastoid breadth, and depth of braincase), with nonsignificant results, and the means for males and females were identical in three measurements (length of maxillary toothrow, interparietal width, and interparietal length).

Liomys salvini.—Males were found to be significantly larger than females in six (total length, length of hind foot, greatest length of skull, zygomatic breadth, interorbital breadth, and length of rostrum) of the 13 measurements tested. Males had the larger mean in five measurements (length of tail, mastoid breadth, length of nasals, depth of braincase, and interparietal length) in which the means were not significantly different; in the remaining two measurements (length of maxillary toothrow and interparietal length), females had the larger mean.

Liomys adspersus.—Males were found to be significantly larger than females in seven (total length, length of tail, greatest length of skull, zygomatic breadth, length of nasals, length of rostrum, and depth of braincase) of the 13 measurements tested. For three of the measurements (length of hind foot, length of maxillary toothrow, and interparietal width) with nonsignificant results, males had the largest mean, and for two (mastoid breadth and interparietal length) males and females had the same means. Females have, on the average, a broader interorbital constriction.

Conclusions.—Males were found to be significantly larger than females in approximately half of the measurements tested and in most of the others where the means were not significantly different, males averaged larger than females. Based upon this information all data dealing with size has been treated separately for the sexes in all of the following analyses.

The finding of significant secondary sexual variation in size in *Liomys* is of interest because no such significant variation has been found (or at least it was not thought to be present) in most measurements of other heteromyid genera studied—*Dipodomys* (Hall and Dale, 1939:49; Hall, 1946:403-433; Setzer, 1949:478; Genoways and Jones, 1971:268), *Perognathus* (Hall, 1946:357-377; Glass, 1947:175; Jones, 1953:518; Baker, 1954:342), and *Microdipodops* (Hall, 1941:241). Lidicker (1960:142-155), however, did find considerable secondary sexual variation in specimens of *Dipodomys merriami* as did Schmidly (1971: 110-111) in specimens of *Dipodomys ordii* from north Texas. In many instances, the one characteristic in which males and females were found to differ most was weight; Genoways and Jones (1971:268) found that males and females of *Dipodomys phillipsii* were significantly different in total length and length of tail, but not in other measurements. The extent and a possible explanation of the signifi-

TABLE 2.—*Secondary sexual variation in external and cranial measurements in four species of* Liomys. *The four species (in the order that they appear in the table) are* Liomys irroratus *from central Jalisco,* Liomys pictus *from western Jalisco,* Liomys salvini *from the departments of Carazo and Managua, Nicaragua, and* Liomys adspersus *from Guánico, Los Santos, Panamá. Statistics given are number, mean, two standard errors of the mean, range, coefficient of variation,* F, *and* F_S. *Means for males and females that are significantly different at* P<.05 *are marked with an asterisk; those that are not significantly different are marked ns.*

Measurements and sex	N	Mean ± 2 SE	Range	CV	F_S / F	
			Liomys irroratus			
Total length						
Male	22	238.0 ± 5.18	(216.0-262.0)	5.1	17.52	*
Female	34	226.1 ± 3.14	(207.0-251.0)	4.0	4.03	
Length of tail						
Male	22	120.1 ± 3.31	(106.0-138.0)	6.5	17.69	*
Female	34	112.5 ± 1.98	(102.0-131.0)	5.1	4.03	
Length of hind foot						
Male	21	29.2 ± 0.49	(26.0-31.0)	3.8	14.27	*
Female	36	28.2 ± 0.27	(27.0-30.0)	2.9	4.02	
Greatest length of skull						
Male	21	32.1 ± 0.49	(30.4-34.1)	3.5	8.21	*
Female	33	31.4 ± 0.21	(30.3-33.0)	2.0	4.03	
Zygomatic breadth						
Male	19	15.6 ± 0.29	(14.8-16.6)	4.0	3.10	ns
Female	27	15.3 ± 0.17	(14.6-16.3)	2.9	4.06	
Interorbital constriction						
Male	22	8.0 ± 0.16	(7.2-8.7)	4.7	10.10	*
Female	35	7.7 ± 0.09	(7.2-8.3)	3.6	4.02	
Mastoid breadth						
Male	21	14.5 ± 0.18	(13.8-15.4)	2.8	4.69	*
Female	33	14.3 ± 0.08	(13.8-14.7)	1.7	4.03	
Length of nasals						
Male	22	12.5 ± 0.28	(11.4-13.4)	5.3	2.10	ns
Female	36	12.2 ± 0.20	(11.0-13.5)	5.0	4.02	

TABLE 2.—*Continued.*

Length of rostrum						
Male	22	14.2 ± 0.27	(13.2-15.4)	4.5	7.36	*
Female	36	13.8 ± 0.13	(13.0-14.9)	2.9	4.02	
Length of maxillary toothrow						
Male	22	5.1 ± 0.07	(4.8-5.4)	3.2	1.25	ns
Female	36	5.1 ± 0.07	(4.4-5.4)	4.0	4.02	
Depth of braincase						
Male	20	8.7 ± 0.12	(8.2-9.2)	3.0	0.16	ns
Female	33	8.6 ± 0.06	(8.2-9.0)	2.1	4.03	
Interparietal width						
Male	21	8.7 ± 0.19	(7.9-9.4)	5.0	2.58	ns
Female	34	8.5 ± 0.13	(7.8-9.5)	4.6	4.03	
Interparietal length						
Male	21	3.6 ± 0.11	(3.0-4.1)	7.1	0.02	ns
Female	34	3.6 ± 0.10	(2.9-4.1)	7.7	4.03	
Liomys pictus						
Total length						
Male	35	241.0 ± 4.12	(218.0-264.0)	5.1	15.80	*
Female	27	229.7 ± 3.72	(212.0-248.0)	4.2	4.00	
Length of tail						
Male	35	123.5 ± 2.80	(105.0-138.0)	6.7	7.27	*
Female	27	118.5 ± 2.21	(108.0-128.0)	4.8	4.00	
Length of hind foot						
Male	40	28.9 ± 0.35	(26.0-31.0)	3.9	1.95	ns
Female	34	28.5 ± 0.41	(26.0-31.0)	4.2	3.98	
Greatest length of skull						
Male	39	32.3 ± 0.24	(30.8-34.1)	2.3	15.76	*
Female	34	31.6 ± 0.26	(30.1-33.0)	2.4	3.98	
Zygomatic breadth						
Male	30	15.0 ± 0.14	(14.1-15.9)	2.6	14.67	*
Female	31	14.6 ± 0.12	(14.1-15.2)	2.4	4.00	
Interorbital constriction						
Male	40	7.8 ± 0.11	(7.1-8.7)	4.4	2.42	ns
Female	35	7.6 ± 0.11	(7.1-8.6)	4.2	3.98	

TABLE 2.—*Continued.*

Mastoid breadth						
Male	39	14.3 ± 0.12	(13.6-15.0)	2.6	2.83	ns
Female	35	14.1 ± 0.11	(13.5-14.8)	2.3	3.98	
Length of nasals						
Male	40	13.1 ± 0.18	(11.7-14.3)	4.4	7.86	*
Female	34	12.7 ± 0.21	(11.1-13.9)	4.7	3.98	
Length of rostrum						
Male	38	14.2 ± 0.16	(13.1-15.5)	3.4	11.81	*
Female	32	13.8 ± 0.18	(13.0-14.8)	3.7	3.99	
Length of maxillary toothrow						
Male	36	4.9 ± 0.06	(4.6-5.4)	3.6	2.63	ns
Female	35	4.9 ± 0.07	(4.4-5.2)	4.1	3.99	
Depth of braincase						
Male	39	8.3 ± 0.07	(7.8-8.9)	2.7	2.66	ns
Female	33	8.2 ± 0.08	(7.7-8.8)	3.0	3.98	
Interparietal width						
Male	39	8.9 ± 0.13	(7.9-9.7)	4.5	0.01	ns
Female	35	8.9 ± 0.16	(7.9-9.5)	5.2	3.98	
Interparietal length						
Male	38	4.5 ± 0.10	(3.8-5.2)	6.7	0.02	ns
Female	35	4.5 ± 0.10	(4.0-5.1)	6.4	3.98	
			Liomys salvini			
Total length						
Male	12	224.8 ± 5.79	(213.0-240.0)	4.5	21.08	*
Female	16	209.1 ± 4.05	(196.0-227.0)	3.9	4.21	
Length of tail						
Male	12	112.2 ± 4.24	(94.0-121.0)	6.5	3.80	ns
Female	16	107.3 ± 2.92	(100.0-121.0)	5.4	4.22	
Length of hind foot						
Male	13	27.0 ± 0.78	(25.0-30.0)	5.2	5.59	*
Female	21	26.0 ± 0.46	(24.0-29.0)	4.0	4.14	
Greatest length of skull						
Male	16	30.9 ± 0.38	(29.3-32.2)	2.5	8.20	*
Female	19	30.2 ± 0.37	(28.7-31.3)	2.7	4.13	

TABLE 2.—*Continued.*

Zygomatic breadth						
Male	12	14.4 ± 0.35	(13.5-15.7)	4.2	5.82	*
Female	15	13.9 ± 0.24	(13.0-14.8)	3.4	4.22	
Interorbital breadth						
Male	17	6.7 ± 0.16	(6.2-7.4)	4.9	5.71	*
Female	23	6.5 ± 0.07	(6.1-6.8)	2.7	4.09	
Mastoid breadth						
Male	16	13.5 ± 0.19	(12.9-14.2)	2.8	0.85	ns
Female	23	13.3 ± 0.17	(12.7-14.2)	3.1	4.11	
Length of nasals						
Male	17	11.8 ± 0.20	(11.0-12.4)	3.6	2.84	ns
Female	21	11.5 ± 0.23	(10.4-12.2)	4.5	4.11	
Length of rostrum						
Male	17	13.3 ± 0.23	(12.4-14.3)	3.6	11.15	*
Female	19	12.8 ± 0.21	(11.9-13.5)	3.5	4.12	
Length of maxillary toothrow						
Male	16	4.5 ± 0.09	(4.2-4.8)	3.8	1.40	ns
Female	24	4.6 ± 0.08	(4.2-5.0)	4.4	4.10	
Depth of braincase						
Male	15	8.3 ± 0.20	(7.6-9.0)	4.6	1.44	ns
Female	21	8.1 ± 0.17	(7.5-9.2)	4.7	4.13	
Interparietal width						
Male	16	8.6 ± 0.25	(7.7-9.5)	5.9	0.86	ns
Female	22	8.7 ± 0.20	(7.6-9.8)	5.4	4.11	
Interparietal length						
Male	16	3.9 ± 0.13	(3.6-4.4)	6.7	0.82	ns
Female	22	3.8 ± 0.14	(3.4-4.7)	8.8	4.11	
Liomys adspersus						
Total length						
Male	18	265.9 ± 5.29	(248.0-285.0)	4.2	10.89	*
Female	6	249.7 ± 5.99	(244.0-264.0)	2.9	4.28	
Length of tail						
Male	18	136.6 ± 3.37	(123.0-148.0)	5.2	5.87	*
Female	6	128.8 ± 4.54	(124.0-138.0)	4.3	4.28	

TABLE 2.—*Continued.*

Length of hind foot						
Male	21	31.4 ± 0.74	(26.0-34.0)	5.4	1.30	ns
Female	8	30.6 ± 0.92	(29.0-32.0)	4.3	4.21	
Greatest length of skull						
Male	20	35.8 ± 0.64	(33.4-38.9)	4.0	4.49	*
Female	7	34.7 ± 0.24	(34.3-35.1)	0.9	4.21	
Zygomatic breadth						
Male	5	17.0 ± 0.33	(16.6-17.4)	2.1	19.88	*
Female	3	16.0 ± 0.23	(15.8-16.2)	1.3	5.59	
Interorbital constriction						
Male	21	7.4 ± 0.12	(7.0-8.0)	3.6	0.28	ns
Female	8	7.5 ± 0.12	(7.3-7.8)	2.2	4.21	
Mastoid breadth						
Male	20	14.5 ± 0.14	(14.0-15.3)	2.1	0.02	ns
Female	8	14.5 ± 0.28	(13.8-15.2)	2.7	4.22	
Length of nasals						
Male	20	15.1 ± 0.31	(13.9-17.3)	4.6	11.49	*
Female	7	14.1 ± 0.32	(13.5-14.8)	3.0	4.22	
Length of rostrum						
Male	14	16.1 ± 0.44	(15.0-17.9)	5.2	5.55	*
Female	5	15.2 ± 0.29	(14.7-15.5)	2.1	4.41	
Length of maxillary toothrow						
Male	20	5.4 ± 0.11	(4.9-5.9)	4.6	0.53	ns
Female	8	5.3 ± 0.15	(5.1-5.6)	3.9	4.22	
Depth of braincase						
Male	20	9.5 ± 0.14	(8.9-10.1)	3.3	6.57	*
Female	8	9.2 ± 0.16	(8.9-9.5)	2.4	4.21	
Interparietal width						
Male	15	8.3 ± 0.22	(7.2-8.9)	5.0	1.19	ns
Female	8	8.1 ± 0.30	(7.5-8.5)	5.2	4.32	
Interparietal length						
Male	19	4.4 ± 0.19	(3.4-4.8)	9.3	0.01	ns
Female	8	4.4 ± 0.27	(4.0-5.2)	8.7	4.24	

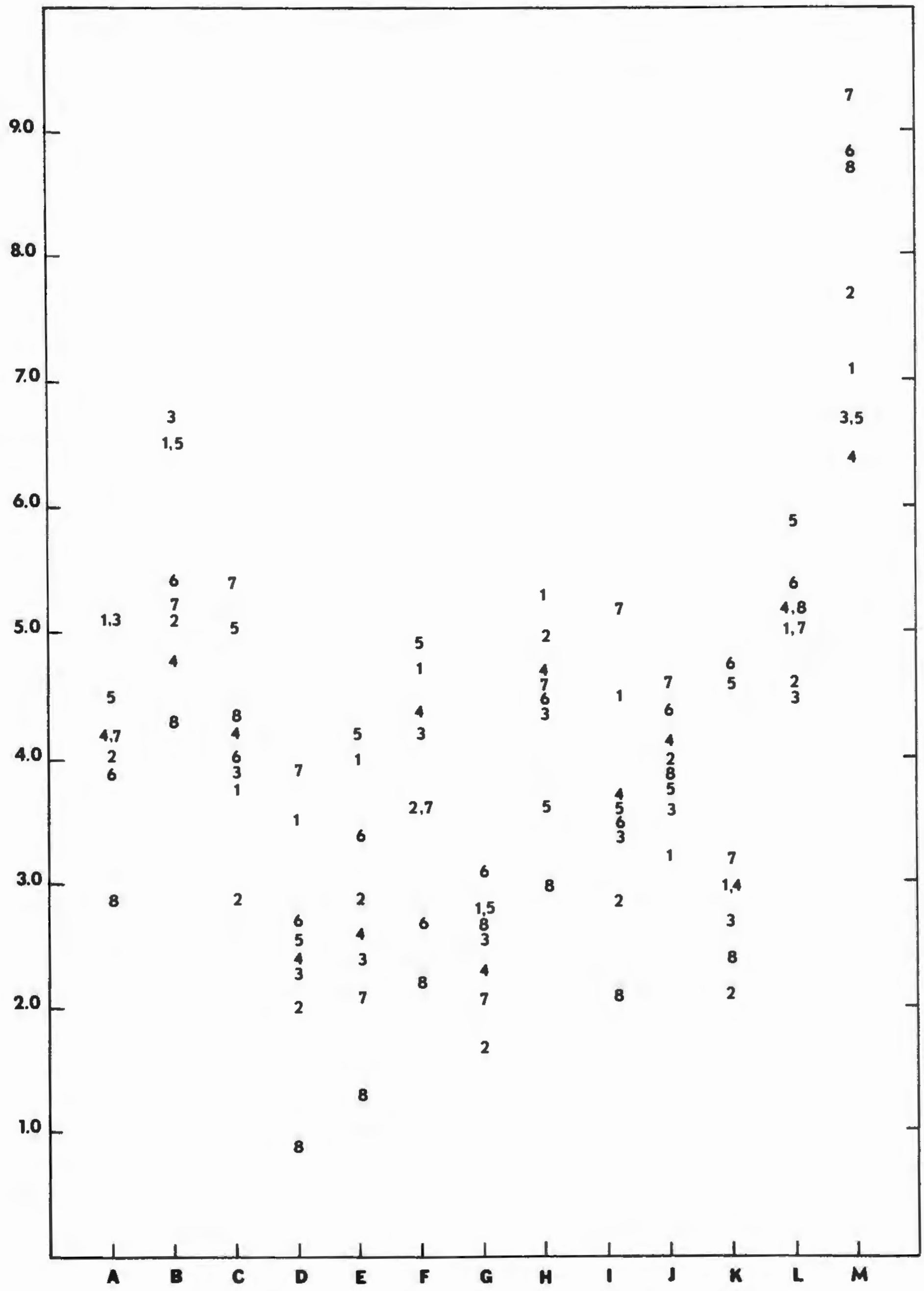


FIG. 4.—Coefficients of variation (ordinate) of external and cranial measurements used in this study. These measurements (abscissa) are as follows: A, total length; B, length of tail; C, length of hind foot; D, greatest length of skull; E, zygomatic breadth; F, interorbital constriction; G, mastoid breadth; H, length of nasals; I, length of rostrum; J, length of maxillary toothrow; K, depth of braincase; L, interparietal width; M, interparietal length. The plotted

cance of secondary sexual variation in this group of rodents and others must await the time that more species have been thoroughly studied.

Individual Variation

External and cranial measurements.—The majority of the measurements used in this study revealed relatively low individual variation in the four species analyzed. Most coefficients of variation were less than 6.0 (Table 2 and Fig. 4); these values are well within limits of those found for other small rodents (Long, 1968, 1969, 1970). Length of the interparietal bone was found to be the most variable parameter tested with coefficients of variation ranging from 6.4-9.3, but width of the interparietal also was found to have relatively high individual variation. The high variability of these two measurements probably resulted from the fact that size and shape of the interparietal bone tends to be rather variable and, most importantly, because measurements were difficult to take, resulting in a relatively low degree of precision. Variation in external measurements averaged greater than in cranial measurements. This undoubtedly resulted from variation in taking of the external measurements by various collectors as pointed out by Sumner (1927:177-181).

Cranial variation.—Individual cranial variations or abnormalities that I found in *Liomys* can be grouped as follows: 1) supernumerary or bregmatic bones, 2) abnormalities resulting from injuries, and 3) dental abnormalities from genetic or developmental sources and disease. Variation in the latter two groups was recorded for all specimens examined, but supernumerary cranial bones were recorded only for specimens stored in the collections of The University of Kansas. These bregmatic bones were found only along the suture between the parietals, at the junction of the frontal and parietal bones, and along the sutures between parietals and the interparietal (Fig. 5). The occurrence of abnormalities is discussed below for each species in which they were found.

Supernumerary bones were noted in only one of the more than 800 specimens examined of *Liomys irroratus*. This specimen was a subadult female from Ejido Santa Isabel, Tamaulipas (KU 57616). Of more than 2700 specimens examined, two were found to have cranial abnormalities resulting from injury (KU 39898, 59532), four individuals exhibited genetic or developmental abnormalities of teeth (UMMZ 96939, UNAM 3053, KU 96021, USNM 32732/44655), six showed dental erosion resulting from caries (KU 109233, 109236, 55908, 99780, 28055, 24011), and two specimens had dental attrition from causes other than caries (MVZ 91313, USNM 81411). Most interesting of these abnormalities was found in an adult female from Tequesquitengo, Morelos, in which the anterior and posterior lophs of the upper left premolar were never fused; however, the enamel covering of each loph was complete as far as could be determined.

numbers refer to taxa as follows: 1, *Liomys irroratus* (males); 2, *Liomys irroratus* (females); 3, *Liomys pictus* (males); 4, *Liomys pictus* (females); *Liomys salvini* (males); 6, *Liomys salvini* (females); 7, *Liomys adspersus* (males); 8, *Liomys adspersus* (females). See also Table 2.

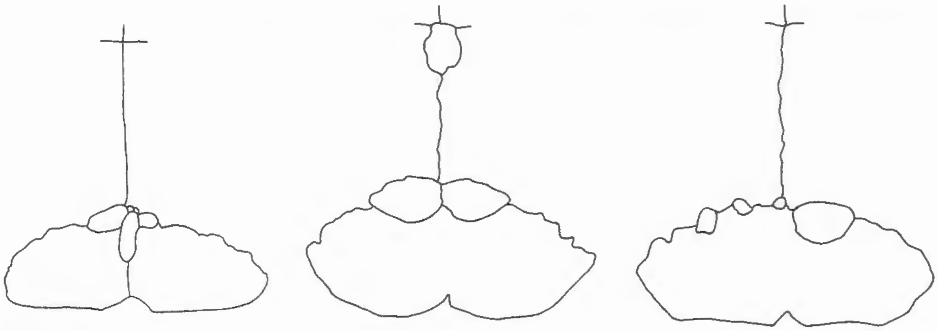


FIG. 5.—Interparietal bone and suture between parietal bones of three specimens of *Liomys pictus* to illustrate size and position of bregmatic bones. The specimens from left to right are KU 85813, Platanares, 10 mi. E Ruiz, Nayarit; KU 96055, 2.2 mi. NE Contla, Jalisco; KU 89497, 3 mi. NE El Fuerte, Sinaloa.

In more than 950 specimens of *Liomys pictus* examined, supernumerary bones were noted in the crania of 16 individuals (Fig. 5). In more than 2850 specimens examined, one was found to have suffered a cranial injury (CAS 14351), three specimens exhibited genetic or developmental abnormalities of teeth (AMNH 172410, CAS 14337, KU 28451), one individual had dental caries (UA 10812), two specimens showed displaced teeth as the result of foreign material being lodged between them (KU 39824, 39829), and one had a high degree of attrition of peridental tissue (KU 62563). One noteworthy specimen was a subadult male from 5 miles south of Chiapa, Chiapas, in which the second upper molar on the left side consisted of a single loph (apparently the anterior).

In nearly 500 specimens of *Liomys salvini* examined, supernumerary bones were found in the cranium of only one specimen, which was from km. 24 on highway S Guatemala City, Guatemala, Guatemala (KU 83964). In a total of more than 1375 specimens of *Liomys salvini* examined, two were found to have cranial abnormalities resulting from injuries (KU 71159, 71181) and two individuals exhibited dental abnormalities resulting from developmental errors (UMMZ 96535, 96539). One (USNM 323670) specimen of *Liomys adspersus* of 194 examined was found to have foreign material lodged between its teeth. No other abnormalities were noted for this species.

External variation.—Little individual or abnormal variation was observed in the external morphology of spiny pocket mice. The only external variation of note was the occurrence of white tips on tails of specimens of *Liomys pictus* from southern Sonora (five of 11 KU specimens from Alamos) and of *Liomys irroratus* from Michoacán (nine of 19 MVZ specimens from 4 mi. S Cuitzeo and two specimens from Pátzcuaro at the same museum).

MOLT

The sequence of molt described below was based on study of specimens of *Liomys pictus* housed in the Museum of Natural History at Kansas. Other species

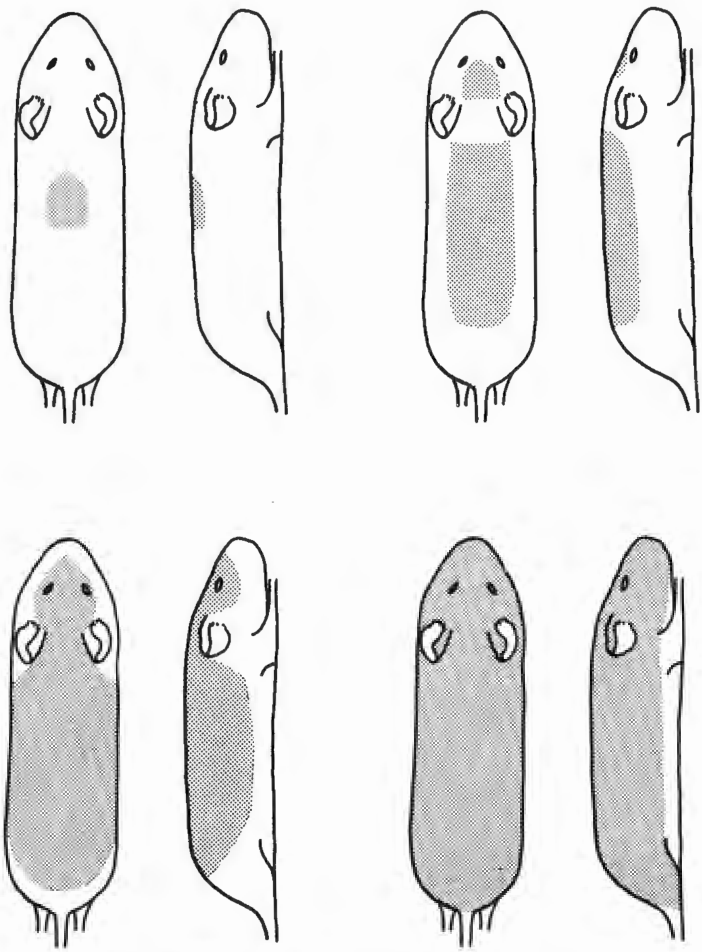


FIG. 6.—Generalized diagram of progression of molt in *Liomys* (from upper left to lower right). This sequence is discussed in text.

of *Liomys* apparently follow a similar pattern of molt. I have seen only two pelages—juvenile and adult—in museum specimens of *Liomys*; however, according to Eisenberg (1963*a*:71) there is another pelage before the one I have termed juvenile. The pattern of molt from juvenile to adult pelage is the same as from one adult pelage to another. Adults molt but once annually.

Molt originates in a middorsal spot approximately one-third of the distance from the ears to the rump (see Fig. 6). From this point molt progresses anteriorly along the middorsal line to just posterior to the ears and posteriorly to one-half to two-thirds the distance to the rump; at the same time, molt lines spread slowly laterally. A second molt center originates on top of the head and spreads to molt around the eyes and onto the rostrum. The two centers of molt are joined in the area between the ears. Molt on the back progresses to the lateral stripe first at a point lateral and just posterior to the ears; at the same time progressing posteri-

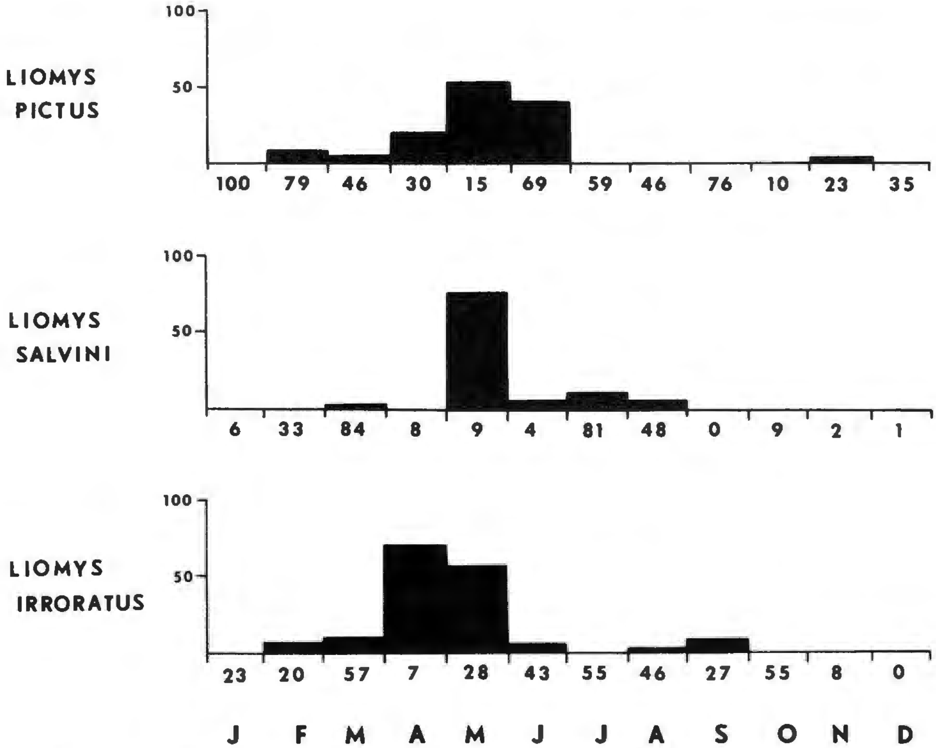


FIG. 7.—Per cent of total number of specimens examined by month that evinced annual molt for three species of *Liomys*. Total number of specimens examined for each month are given at the appropriate place under the histograms.

orly in the middorsal region. Molt is next completed on the cheeks and lateral to the ears; finally the rump will be molted. I have never seen the line of molt on a specimen where it has progressed beyond the lateral stripe onto the venter. Either the venter molts in a different pattern, which I have not been able to detect, or else molt occurs there by replacement of individual hairs rather than in any distinct pattern. Except for the sequence on the venter, this pattern of molt is similar to that found in *Perognathus parvus* (Speth, 1969) and, according to the terminology proposed by Ling (1970:31), is a ventrad type molt pattern.

The timing of molt from one adult pelage to another in three species of *Liomys* is compared in Fig. 7. Although there are some differences, these three species—*pictus*, *salvini*, and *irroratus*—appear to molt at approximately the same time of year. In all three, a high percentage of individuals are actively molting in May. In *L. pictus*, large numbers of individuals also were found molting in April and June; a few were molting as early as January and one individual was molting in November (this specimen was in extremely worn pelage, which suggests to me that it either was late in molting and was completing molt that should have taken place in May or June or that it had worn its new pelage rapidly and some mechanism was triggered causing the animal to undergo another molt). Triggering of an early molt when the pelage is heavily worn may explain why a few individuals molt early (in January and February). Besides the high percentage molting in May, specimens of *L. salvini* were found molting in March, June, July, and August. The highest per cent of specimens of *Liomys irroratus* undergoing molt was in April. Fleming (1970:477), who studied *Liomys adspersus* in the Canal Zone, found specimens molting in January, April, May, June, August, and September, with the majority molting in May and June. He also examined series of *L. adspersus* from the Pacific slope of western Panamá in which many of the specimens were molting in January and February. Based upon my data and that of Fleming, I conclude that adult *Liomys* ordinarily undergo a single molt annually and that a majority of the members of each species molt in the period of April to June.

SYSTEMATIC ACCOUNTS

Genus LIOMYS

1902. *Liomys* Merriam, Proc. Biol. Soc. Washington, 15:44, 5 March.

Type species.—Heteromys alleni Coues (= *Liomys irroratus alleni*).

Diagnosis

Cheek teeth medium crowned; upper incisors asulcate; only two lophids on lower premolar; accessory enamel island on molars present only for short period (visible only in unworn molars); entostyle closely united to hypocone so that Y-shape of median valley of upper premolar is poorly formed; auditory region uninflated; pelage hispid, consisting of stiff spines mingled with slender soft hairs; soles of hind feet haired; interpterygoid fossa U-shaped anteriorly; specialized claw on hind foot; adapted for scampering.

Comparisons

Compared with members of the other genus in the subfamily Heteromyinae, *Heteromys,* species of *Liomys* can be distinguished as follows: cheek teeth lower crowned; lower premolar with two lophids instead of three or four; accessory enamel islands visible only in unworn molars (rather than persisting in some taxa until adulthood); entostyle on upper premolar closely united with hypocone (this condition varied depending upon species involved) so that median valley only slightly Y-shaped as compared with entostyle well separated from hypocone so that median valley is Y-shaped; interpterygoid fossa U-shaped anteriorly instead of V-shaped; soles of hind feet haired instead of naked (except in *H. gaumeri*); specialized claw on hind foot larger (see Goodwin, 1945).

Key to Species of Liomys

1. Five plantar tubercles (Fig. 58); pterygoid bones with broad wings (Fig. 61); shaft of baculum oval to tip (Fig. 56); glans penis long (more than 75 per cent) in comparison with baculum (Fig. 54); 60 chromosomes (Fig. 59); no neck between head and midpiece of spermatozoon (Fig. 57); parasitized by the anoplurans *Fahrenholzia ehrlichi* and *Fahrenholzia texana*; upper parts grayish brown, lateral stripe pale pinkish to buffy; occurring on Mexican Plateau and in adjacent areas of northern and central México, south as far as south-central Oaxaca (Fig. 17) .... *Liomys irroratus,* p. 47

1'. Usually six plantar tubercles (Fig. 58); pterygoid bones with narrow wings (Fig. 61); shaft of baculum either flattened dorsoventrally or flattened dorsoventrally and compressed laterally at some point (Fig. 56); glans penis short (less than 75 per cent) in comparison with baculum (Fig. 54); 48 or 56 chromosomes (Fig. 59); neck present between head and midpiece of spermatozoon (Fig. 57); parasitized by Anoplura other than *F. ehrlichi* and *F. texana*; upper parts either reddish brown or chocolate brown, or somewhat paler, with either an ochraceous lateral stripe or lateral stripe absent; not occurring on the Mexican Plateau 2

2. Upper parts reddish brown with an ochraceous lateral stripe; interorbital region broad in comparison with greatest length of skull (Tables 11 and 19; Fig. 46); distal end of the shaft of the baculum with a laterally compressed ventral keel and just posterior to this region, the shaft is flattened dorsoventrally (Fig. 56); tip of glans penis long when compared with its total length (Fig. 54); urethral lappets trilobed (Fig. 55); 48 chromosomes

(Fig. 59); head of spermatozoon long and with pointed apex (Fig. 57); hairs on back not curled upward and not visible above spines; occurring along the Pacific slope of western México as far south as the vicinity of Tonalá, Chiapas, in the central valley of Chiapas, and in the southern half of Veracruz 3

2'. Upper parts chocolate brown to somewhat paler, lateral stripe absent; interorbital region narrow in comparison with greatest length of skull (Tables 21 and 27; Fig. 46); shaft of baculum dorsoventrally flattened just posterior to slightly upturned tip, no laterally compressed ventral keel present; tip of glans penis short when compared with its total length (Fig. 54); urethral lappets bilobed (Fig. 55); 56 chromosomes (Fig. 59); head of spermatozoon short and with a bluntly rounded apex (Fig. 57); hairs on back curled upward and visible above the spines; occurring in Central America and into México along the Pacific coast as far as the vicinity of Reforma, Oaxaca 4

3. In southeastern Jalisco, size small (greatest length of skull, 28.9 to 32.0—see Table 11), (specimens approaching *L. spectabilis* in size do occur in Guerrero and Oaxaca but these are still slightly smaller and have a proportionally deeper braincase); in Jalisco hind foot rarely more than 30; laterally compressed ventral keel on baculum short, 0.85 to 1.25 (Fig. 56); fundamental number of chromosomes 66 (Fig. 59); head of spermatozoon similar to that of *L. spectabilis*, but significantly shorter and narrower (Fig. 57); occurring along Pacific coast of western México, in the central valley of Chiapas, and in southern Veracruz (Fig. 28) .... *Liomys pictus*, p.124

3'. In southeastern Jalisco, size large (greatest length of skull, 33.0 to 35.3—see Table 19); hind foot rarely less than 30; laterally compressed ventral keel on baculum relatively long, 1.30 (Fig. 56); fundamental number of chromosomes 64 (Fig. 59); head of spermatozoon similar to that of *L. pictus*, but significantly longer and broader (Fig. 57); occurring only in southeastern Jalisco (Fig. 30) .... *Liomys spectabilis*, p.195

4. Size small (greatest length of skull averaging less than 33.5—see Table 21); fundamental number of chromosomes 86 (Fig. 59); morphology of head and neck of spermatozoon similar to that of *L. adspersus*, but head significantly broader and neck significantly shorter (Fig. 57); occurring from southern Oaxaca to central Costa Rica (Fig. 40) .... *Liomys salvini*, p.202

4'. Size large (greatest length of skull averaging over 34.5—see Table 27); fundamental number of chromosomes 84 or less (Fig. 59); morphology of head and neck of spermatozoon similar to that of *L. salvini*, but head significantly narrower and neck significantly longer (Fig. 57); occurring only in central Panamá (Fig. 45) .... *Liomys adspersus*, p.246

It is difficult to construct a useful key to members of the genus *Liomys* because some of the most easily observed characters, external and cranial measurements, exhibit a high degree of geographic variation within individual species. However, one fact that does help to simplify this problem is that zones of sympatry between species of the genus are restricted; therefore, chances are rather low that more than one species will be collected at any one locality. Of the five species herein recognized, only in southeastern Jalisco is there a possibility of obtaining as many as three (*irroratus*, *pictus*, and *spectabilis*) together (all three have not yet been taken together there). *Liomys irroratus* and *Liomys pictus* occur sympatrically in a zone from central Jalisco southward through Michoacán, in the vicinity of the Balsas Basin and Sierra Madre del Sur of Guerrero, and along the Sierra Madre of Oaxaca. However, even within this area the two species many times are microallopatric (Smith, 1965:57) with *irroratus* inhabiting the uplands and *pictus* the lower and generally more mesic situations. Specimens of *L. pictus* and *L. salvini* have been taken sympatrically from the vicinity of Reforma in southeastern

Oaxaca to the vicinity of Tonalá in northwestern Chiapas. Aside from these cases of sympatry, I am aware of no others and, unless some rather extensive extensions of known ranges are discovered, I do not expect there to be others. Data on mensural relationships of the species in zones of sympatry are presented in the discussion of external and cranial morphology in the section on Specific Relationships following the accounts of species.

Following the accounts of the Recent species of *Liomys* is a short discussion on the status of the nominal fossil species, *Liomys centralis*.

Liomys irroratus

Mexican Spiny Pocket Mouse

This species occurs on the Mexican Plateau and in adjacent areas. In the northeastern part of its geographic range, *Liomys irroratus* extends into southern Texas and, in the northwest, specimens have been recorded from southern Chihuahua east of the Sierra Madre Occidental. From Chihuahua the species occurs southward to central Michoacán, generally to the east of the Sierra, and, along the east coast it is known from as far south as central Veracruz. The species occurs in the vicinity of the Transverse Volcanic Belt and southward into Puebla, Guerrero, and Oaxaca. The southernmost record for the species is Zapotitlán, Oaxaca.

Diagnosis

Generally medium-sized for the genus in external and cranial measurements, although some populations are relatively large (*guerrerensis*) and others quite small (*torridus*); cranium relatively broad in comparison with length; protoloph of upper permanent premolar composed of three discernable cusps; metaloph of upper premolar with three cusps (hypocone largest, metacone only slightly smaller than hypocone); entostyle distinct but not widely separated from hypocone; re-entrant angle on labial side of lower premolar not united with median valley; baculum simple, with large rounded base, oval-shaped shaft, and slightly upturned tip (extreme tip of baculum may be slightly laterally compressed); glans penis relatively long in comparison with length of baculum; structure of glans simple, with little sculpturing; urethral lappets trilobed; 2N = 60, FN = 62; head of spermatozoon long and with relatively pointed apex, no neck discernable between head and midpiece of spermatozoon; wings of pterygoids relatively broad; parasitized by the anopluran species, *Fahrenholzia ehrlichi* and *Fahrenholzia texana*; five plantar tubercles; upper parts grayish brown; lateral stripe, which is usually present, generally pale pink to buff; underparts white; hairs on back not curled upward so as to be conspicuous above spines.

Comparisons

Specimens of *Liomys irroratus* usually can be distinguished from those of *Liomys pictus* in areas of sympatry by their generally larger external and cranial size (not always true because of geographic variation within each species—see the discussion of external and cranial morphology in the section on specific relationships where the two species are compared from four areas of sympatry). Depth of braincase, which averaged deeper in *irroratus* in all analyses, was heavily weighted in the four discriminant function analyses comparing *irroratus* and *pictus*. The cusps of the metaloph of the upper permanent premolar of *irroratus* are distinct and the entostyle is not connected to the hypocone by a distinct loph as in *pictus*. The baculum of *irroratus* has an ovoid shaft to the slightly upturned tip, at which point a small area may be laterally compressed, whereas the baculum of *pictus* has a terminal ventral keel that is laterally compressed and a section of the shaft has been dorsoventrally flattened posterior to the keel. The glans penis of *irroratus* can be distinguished from that of *pictus* by its greater length in comparison with the length of the baculum, shorter tip, and less external sculpturing. The karyotype of *L. irroratus* reveals 60 chromosomes with a fundamental number of 62, whereas the karyotype of *L. pictus* possesses 48 chromosomes and a fundamental number of 66. The spermatozoon of *irroratus* possesses a more rounded apex than that of *pictus*; the head of the sperm of *irroratus* is significantly broader than that of *pictus* and a neck is lacking between the head and midpiece in *irroratus*. Other characteristics by which *irroratus* can be distinguished from *pictus*, include broad (rather than narrow) wings on the pterygoid bones (a good character for identification of crania), five instead of usually six plantar tubercles, parasitized by the lice *Fahrenholzia ehrlichi* and *Fahrenholzia texana* rather than by *Fahrenholzia microcephala*, and upper parts grayish brown with a pale pinkish to buffy lateral stripe as opposed to upper parts reddish brown with an ochraceous lateral stripe.

Liomys irroratus can be distinguished from *Liomys spectabilis* by its smaller external measurements, smaller measurements of cranial length, and relatively greater measurements of cranial breadth (based upon *irroratus* material from near the range of *spectabilis*). The baculum of *irroratus*, with its ovoid shaft and slightly upturned tip (a small area of which may be laterally compressed), differs markedly from that of *spectabilis*, which is similar to *pictus* in having a terminal ventral keel that is laterally compressed and, posterior to the keel, a section of the shaft that is dorsoventrally flattened. The glans penis of *irroratus* can be distinguished from that of *spectabilis* by its greater length in comparison with the length of the baculum, shorter tip, and less external sculpturing. The karyotype of *irroratus* has 60 chromosomes and a fundamental number of 62, whereas that of *spectabilis* has 48 chromosomes and a fundamental number of 64. The spermatozoon of *irroratus* differs from that of *spectabilis* in having a more rounded apex on the head and in lacking a neck between the head and midpiece. Other characteristics by which *irroratus* can be distinguished from *spectabilis* include broad (rather than narrow) wings on the pterygoid bones, five instead of six plantar tubercles, and upper parts grayish brown with a pale pinkish to buffy lateral stripe as opposed to upper parts reddish brown with an ochraceous lateral stripe.

Liomys irroratus is distinguishable from *Liomys salvini* by its larger external and cranial measurements—especially noticeable for the three external measurements and interorbital constriction (based on comparative specimens from Oaxaca and Chiapas). The entostyle on the upper premolar is less distinctly separated from the remaining cusps in *irroratus* than in *salvini*, and the re-entrant angle on the labial margin of the lower premolar reaches the medial valley in *salvini* but not *irroratus*. The baculum of *irroratus* has an oval shaft and slightly upturned tip (a small area of which may be laterally compressed), whereas the baculum of *salvini* has a section of the shaft dorsoventrally compressed just posterior to the slightly upturned tip. The glans penis of *irroratus* can be distinguished from that of *salvini* by its greater length in comparison with the length of the baculum and much less external sculpturing, and the urethral lappets of *irroratus* are trilobed, whereas those of *salvini* are bilobed. The karyotype of *irroratus* has 60 chromosomes and a fundamental number of 62 as opposed to 56 chromosomes and a fundamental number of 86 for *salvini.* The spermatozoon of *irroratus* is long with a slightly rounded apex, whereas that of *salvini* is short with a blunt, broadly rounded apex, and the sperm of *irroratus* lacks a neck between the head and midpiece that is present in *salvini.* Other characteristics by which *irroratus* can be distinguished from *salvini* include broad, rather than narrow, wings on the pterygoid bones, five instead of six plantar tubercles, parasitized by the lice *Fahrenholzia ehrlichi* and *Fahrenholzia texana* rather than by *Fahrenholzia fairchildi,* and upper parts grayish brown with a pale pink to buffy lateral line as opposed to upper parts chocolate brown or paler with no lateral line. The hairs on the back of specimens of *salvini* are curled upward and are visible above the spines, which is not true of specimens of *irroratus.*

From *Liomys adspersus, Liomys irroratus* can be distinguished by its smaller cranial measurements except for mastoid breadth and especially interorbital breadth; *irroratus* also has a larger interparietal bone. The entostyle on the upper premolar is less distinctly separated from the remaining cusps in *irroratus* than in *adspersus,* and the re-entrant angle on the labial margin of the lower premolar reaches the median valley in *adspersus* but not in *irroratus.* The oval-shafted baculum of *irroratus* with its slightly upturned tip differs from that of *adspersus* in the same ways it did from the baculum of *salvini* in that both species have a dorsoventrally flattened area. The glans penis of *irroratus* can be distinguished from that of *adspersus* by its greater length in comparison with the length of the baculum and much less external sculpturing. The urethral lappets of *irroratus* are trilobed rather than bilobed. The karyotype of *irroratus* has 60 chromosomes and a fundamental number of 62 as compared with 56 chromosomes and a fundamental number of 84 (possibly as low as 80) for *adspersus.* The spermatozoon of *irroratus* differs from that of *adspersus* in the same manner as from *salvini.* Other characteristics by which *irroratus* can be distinguished from *adspersus* include broad rather than narrow wings on the pterygoid bones, five instead of six plantar tubercles, parasitized by the lice *Fahrenholzia ehrlichi* and *Fahrenholzia texana* rather than by *Fahrenholzia fairchildi,* upper parts grayish brown with a pale pink to buffy lateral line as opposed to upper parts chocolate brown or paler with no lateral stripe, and the hairs on back not curled upward and not visible above the spines.

Ecology

The Mexican spiny pocket mouse occupies an extensive geographic range from southern Texas to southern Oaxaca. The species occurs at sea level along the coasts of Tamaulipas and Veracruz to nearly 10,000 feet on Cerro San Felipe and Mount Zemoaltepec in Oaxaca. The species usually is restricted to relatively dry situations and this is especially noticeable when contact is made with the geographic range of *Liomys pictus.* In such situations *pictus* occurs in lower more mesic areas, whereas *irroratus* is found in the drier upland areas (see the account of *L. pictus* for additional discussion). Although *Liomys irroratus* prefers relatively arid habitats, it does not appear to occur in those areas of the north-central

Mexican Plateau that receive less than 500 millimeters of rainfall annually (see Vivó Escoto, 1964: fig. 10).

No comprehensive ecological study of *L. irroratus* has been undertaken, but ecological information about the species can be found in Alvarez (1963:432-434), Bailey (1905:127), Baker and Greer (1962:104), Baker *et al.* (1967:225-226), Dalquest (1953:122), Davis (1944:389; 1960:151), Davis and Russell (1954:73), Hall and Dalquest (1963:284-286), Hooper (1953:5), Koestner (1941:9, 12), and Villa-R. (1953:407-408). Discussed below are 10 localities from throughout the geographic range of *irroratus* that indicate the type of situations in which this species is found.

Soto la Marina, 100 ft., Tamaulipas.—This locality, on the coastal plains of Tamaulipas, was visited from 15 to 25 May 1953 by Gerd Heinrich, a field representative of the Museum of Natural History at Kansas. The vegetation was tropical deciduous forest with mesquite and other thorny shrubs in the uplands and gallery forest along the rivers. Spiny pocket mice were obtained in traps set in dense brush along the edges of cultivated fields. Other small mammals collected at this place were *Didelphis virginiana, Sylvilagus floridanus, Lepus californicus, Spermophilus mexicanus, Sciurus aureogaster, Perognathus merriami, P. hispidus, Peromyscus leucopus, Onychomys leucogaster, Sigmodon hispidus*, and *Neotoma micropus.*

Sierra de Tamaulipas, 2 mi. S, 10 mi. W Piedra, 1200 ft., Tamaulipas.—The Sierra de Tamaulipas is an isolated system of low mountains rising to about 1000 meters out of the coastal plains of Tamaulipas. Gerd Heinrich visited this area in June 1953 and made a major collection at this location. The vegetation of the area was generally dry, open pine-oak forest. Specimens of the Mexican spiny pocket mouse were trapped in a variety of situations including in the pine-oak forest, along a rock fence, and among the rocks of a dry arroyo. Specimens of other small mammals taken included *Didelphis virginiana, Cryptotis parva, Sylvilagus floridanus, Sciurus aureogaster, Oryzomys melanotis, O. palustris, Reithrodontomys fulvescens, Peromyscus boylii, P. leucopus, P. pectoralis, Sigmodon hispidus, Neotoma micropus*, and *Spilogale putorius.*

Jaumave, 2400 ft., Tamaulipas.—Jaumave lies in a dry valley in the Sierra Madre Oriental. The vegetation on the higher slopes consisted of low oak, but in the valley mesquite was abundant, especially along a stream. In addition, acacia, mimosas, agave, cacti, and other thorny vegetation as well as cultivated crops were generally distributed in the valley. Heinrich found spiny pocket mice to be abundant here with specimens being obtained in most traplines. Other species of mammals obtained were *Notiosorex crawfordi, Oryzomys palustris, Reithrodontomys fulvescens, Peromyscus leucopus, Baiomys taylori, Sigmodon hispidus, Mephitis macroura*, and *Mustela frenata.*

3 mi. W Gutiérrez Zamora, 300 ft., Veracruz.—W. W. Dalquest worked at this locality on the coastal plains of Veracruz from 6 to 9 November 1947. In areas not under cultivation the vegetation consisted of tropical deciduous scrub with acacia and other thorny bushes being the dominant vegetation. There were stands of tall grass in open areas and 30 foot gallery forest along the streams. Dalquest had relatively poor success trapping in this area as traplines set in the acacia scrub and tall grass yielded no small mammals. Specimens of *Liomys irroratus* were obtained in a cornfield where small burrows, evidently occupied by the spiny pocket mice, were observed. Other rodents collected at this locality included *Sciurus deppei, Peromyscus leucopus, P. mexicanus*, and *Sigmodon hispidus.*

2 6/10 mi. E Etzatlán, 4300 ft., Jalisco.—This locality in northwestern Jalisco is just west of the valley of Lago de Magdalena. The area was under heavy agricultural use, with many cornfields and pastures for cattle. P. L. Clifton, field collector for the Museum of Natural History, visited this place on the night of 12 September 1963 and set traps along a rock fence, heavily overgrown with vines and small trees, separating a pasture from a weedy cornfield. Single specimens of *Marmosa canescens* and *Reithrodontomys fulvescens* were the only small mammals taken in addition to 14 *Liomys irroratus.*

2 mi. N Amatitán, 4050 ft., Jalisco.—This locality is in an agricultural area northwest of Guadalajara where agave or maguey is raised for the production of tequila. The vegetation in undisturbed areas was low stands of oak on the hills with pine at higher elevations and grass in the valleys. Clifton, who visited this place on 19 January 1966, set his traps among the weeds and brush along a rock fence between two cornfields. Specimens of two other species of small rodents, *Reithrodontomys fulvescens* and *Baiomys taylori,* were taken in this trapline along with *L. irroratus.*

6 mi. E Querétaro, 7400 ft., Querétaro.—This place was visited on 16 July 1952 by a field party from The University of Kansas. Camp was made on a hillside covered with thorny scrub vegetation with an understory of grass. Traps were placed in a variety of areas including along a rock fence, among the rocks of a volcanic outcrop, under large prickly pear cacti, and in scrub forest. In addition to *L. irroratus,* specimens of *Reithrodontomys fulvescens, Peromyscus boylii, P. truei,* and *Baiomys taylori* were obtained.

1 mi. SSW Tilapa, 3700 ft., Puebla.—The vegetation at this place consisted mainly of arid thorny forest with scattered organ and other cacti. Much of the surrounding area was under cultivation being planted to sugar cane. R. W. Dickerman, who worked at this location on 12-13 August 1954, placed his traps in rocks and brush near a river. No other small mammals were taken in the traps along with *L. irroratus,* but specimens of *Orthogeomys grandis* were taken in gopher sets made near the road above the river.

Omilteme, 7300 ft., Guerrero.—This locality was visited by P. L. Clifton from 13 to 20 July 1964 and by E. C. Birney, L. C. Watkins, and me from 31 July to 3 August 1969. The small village of Omilteme is located in a deep north-south oriented valley in the Sierra Madre del Sur of Guerrero. In the valley, deciduous trees grew along a large stream and grass dominated open areas. On the steep slopes, the forest consisted mostly of pine although some large oak trees were seen in moister areas. The specimens of *Liomys irroratus* were taken on a slope to the north of the village under a stand of pine trees. The ground was covered with a thick layer of pine needles and the understory was only about two feet tall and not dense. Small mammals were relatively abundant with specimens of the following species being obtained in addition to the spiny pocket mice: *Sorex saussurei, Cryptotis goldmani, Sylvilagus cunicularius, S. insonus, Sciurus aureogaster, Oryzomys alfaroi, O. fulvescens, Reithrodontomys fulvescens, Peromyscus boylii, P. megalops, P. thomasi,* and *Neotoma mexicana.*

2 mi. SE Matatlán, 5950 ft., Oaxaca.—On the night of 23 July 1953 a field party from The University of Kansas headed by R. H. Baker visited this locality, which is at the southern edge of the valley of Oaxaca. Camp was made on a limestone hill where the vegetation consisted of low oaks and other scrub vegetation with an understory of grass. In 300 traps, four specimens of *Liomys irroratus,* one of *Reithrodontomys sumichrasti,* five of *Peromyscus truei,* and 14 of *Baiomys musculus* were obtained.

Geographic Variation

Univariate Analysis

Nearly all adult specimens from throughout the geographic range of *Liomys irroratus* were grouped into 36 samples for males and 39 samples for females as follows (see also Fig. 8): *sample 1*—Texas (Brownsville, Edinburg, Elsa, Lomita Ranch, McAllen, San Benito); *sample 2*—Tamaulipas (Bagdad, Matamoros, Reynosa); *sample 3*—Nuevo Leon (General Terán, Linares, Monterrey) and Tamaulipas (N or E Ciudad Victoria, Cruillas, Hidalgo, La Pesca, Marmolejo, Mulato, San Fernando, Soto la Marina); *sample 4*—Tamaulipas (Piedra); *sample 5*—Tamaulipas (Altamira, Antiguo Morelos, Ciudad Victoria and S, Gómez

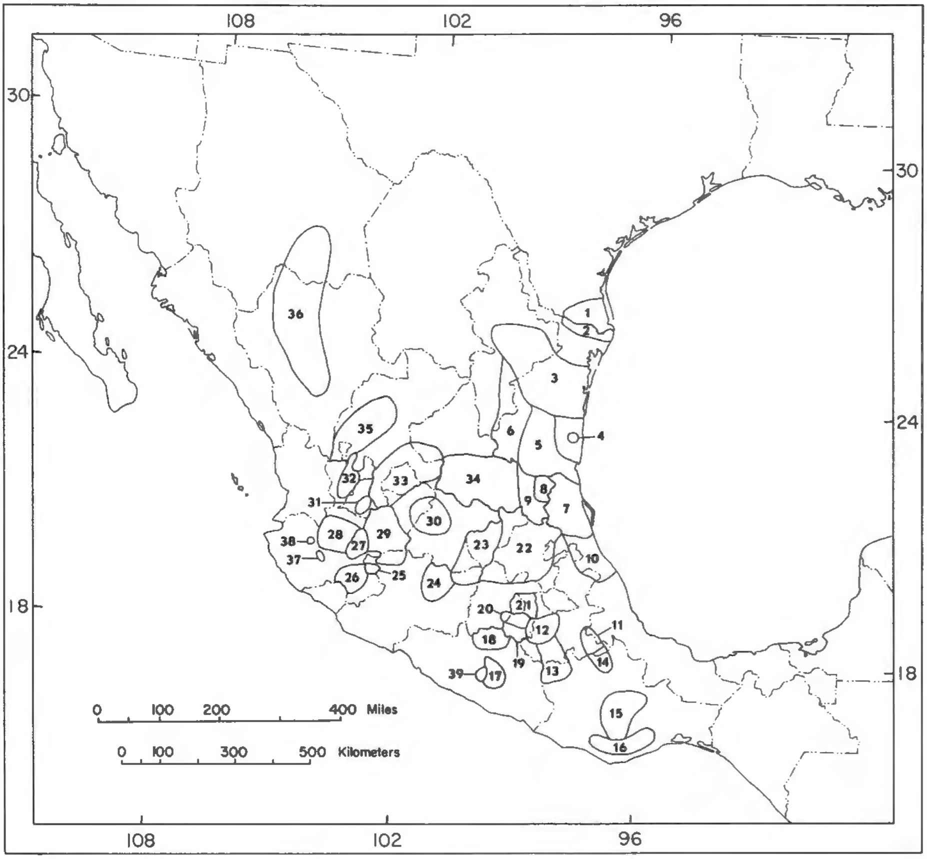


Fig. 8.—Approximate geographic areas included in the 39 samples of *Liomys irroratus*. See test for localities included in each sample.

Farías, El Limón, Quintero); *sample 6*—Nuevo Leon (Aramberri, Ascensión, Iturbide, Pablillo, Zaragoza) and Tamaulipas (Jaumave, Miquihuana, Nicolás, Palmillas); *sample 7*—Veracruz (Ixcatepec, La Mar, Ozuluama, Platón Sánchez, Potrero Llano, south of Tampico [Tamaulipas], Tihuatlán, Tuxpan); *sample 8*—San Luis Potosi (Ajinche, Ebano, Tamuín); *sample 9*—San Luis Potosi (Apetsco, El Sabinito, Huichihuayán, Platanito, Tamazunchale, Valles); *sample 10*—Puebla (Metlaltoyuca, Zihuateutla) and Veracruz (Gutíerrez Zamora, Miahuapan, Nautla, Papantla, San Marcos, Tlapacoyan); *sample 11*—Puebla (Tehuacán, Tepanco) and Veracruz (Acultzingo); *sample 12*—Morelos (Axochiapan, Jonacatepec) and Puebla (Izúcar de Matamoros, Puebla, Tilapa); *sample 13*—Oaxaca (Huajuapan de León, Tlapancingo) and Puebla (Acatlán, Piaxtla, Tehuitzingo); *sample 14*—Oaxaca (Cuicatlán, Teotitlán); *sample 15*—Oaxaca (Cerro San Felipe, Ejutla, Matatlán, Miahuatlán, Mitla, Monte Alban, Mt. Zempoaltepec, Oaxaca, Tlacolula, Yalalag); *sample 16*—Oaxaca (Juchatengo, km. 177.2 Oaxaca-Puerto Escondido Road, Río Jalatengo, Río Jalatengo, Río Molino, San Pedro Jilotepec, Santo Tomás Quierí); *sample*

17—GUERRERO (Agua del Obispo, Almolonga, Chilpancingo, Mazatlán, Xochipala, Zumpango); *sample 18*—GUERRERO (Chapa, Iguala, Los Sabinos, Taxco, Teloloapan, Texcalzintla, Yerbabuena); *sample 19*—MORELOS (Alpuyeca, Cuernavaca [12 mi. S], Huajintlán, Michapa, Puente de Ixtla, Temilpa, Tequesquitengo, Tetecala); *sample 20*—MEXICO (Tenancingo) and MORELOS (Cuernavaca, Huitzilac, Tepoztlán, Yautepec); *sample 21*—DISTRITO FEDERAL (México, San Gerónimo, San Gregorio Altapulco, San Mateo Xalpa, Tlalpan, Zapotitlán) and MEXICO (Cerro La Caldera, San Rafael, Texcoco, Tlalpizahua, Zoquiapan); *sample 22*—HIDALGO (Actopan, Epazoyucan, Ixmiquilpan, Marqués, Zimapán), MEXICO (Atlacomulco), QUERETARO (Jalpan, Pinal de Amoles), and VERACRUZ (Jacales); *sample 23*—GUANAJUATO (Acámbaro), MICHOACAN (Queréndaro), and QUERETARO (Cadereyta, Querétaro, Tolimán); *sample 24*—MICHOACAN (Cuitzeo, Pátzcuaro, Quiroga); *sample 25*—JALISCO (Mazamitla—this sample contains only females); *sample 26*—JALISCO (Ciudad Guzmán, Jazmín, Las Canoas, Sierra Nevada de Colima, Zapotiltic); *sample 27*—JALISCO (Acatlán, Atemajac, Chapala, Guadalajara, Santa Cruz de las Flores); *sample 28*—JALISCO (Amatitán, Ameca, Etzatlán, La Primavera, San Marcos, Tala, Teuchitlán); *sample 29*—JALISCO (Ayo el Chico, Huascata, Ocotlán, Tepatitlán, Yahualica, Zapotlanejo) and MICHOACAN (La Palma, Zamora); *sample 30*—JALISCO (Comanja de Corona, Lagos de Moreno, Unión de San Antonio) and GUANAJUATO (Silao); *sample 31*—ZACATECAS (Moyahua, Santa Rosa); *sample 32*—JALISCO (Bolaños, Mezquitic, Villa Guerrero); *sample 33*—AGUASCALIENTES (Calvillo, Chicalote, La Labor), JALISCO (Belén de Refugio, Encarnación de Díaz), SAN LUIS POTOSI (Cerro Peñon Blanco, Ramos), and ZACATECAS (Berriozábal, Jalpa, Zacatecas); *sample 34*—SAN LUIS POTOSI (Ahualulco, Alvarez, Arriaga, Bledos, Hda. Angostura, Hda. Capulín, Hda. La Parada, Jesús María, Río Verde, San Luis Potosí, Villar); *sample 35*—JALISCO (Huejuquilla) and ZACATECAS (Hda. San Juan Capistrano, Rancho Grande, Río Grande, Saín Alto, Valparaíso); *sample 36*—CHIHUAHUA (Parral, Santa Rosalía) and DURANGO (Chorro, Durango, Indé, Tepehuanes); *sample 37*—JALISCO (Soyatlán del Oro—this sample contains only one adult female); *sample 38*—JALISCO (La Laguna [Sierra de Juanacatlán]—this sample contains only two adult females); *sample 39*—GUERRERO (Omilteme).

Included in these samples are specimens that formerly were known under the names *Liomys bulleri* and *Liomys guerrerensis*. Reasons for inclusion of these taxa in a single species will be discussed in the following sections. Dice grams have been prepared for four measurements (Fig. 9) in order to demonstrate trends in geographic variation. Table 3 gives standard statistics for samples of males and females from all geographic samples.

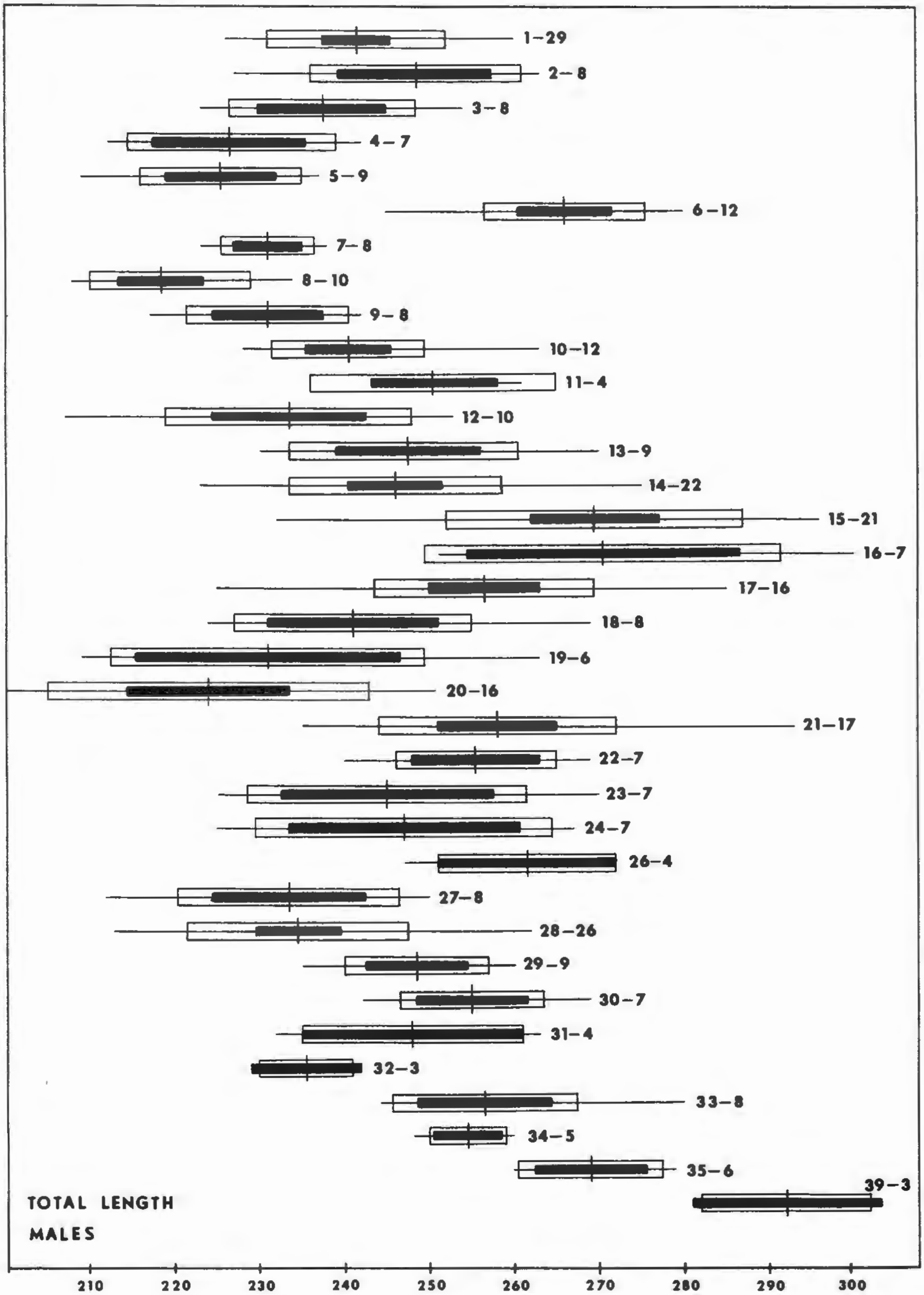
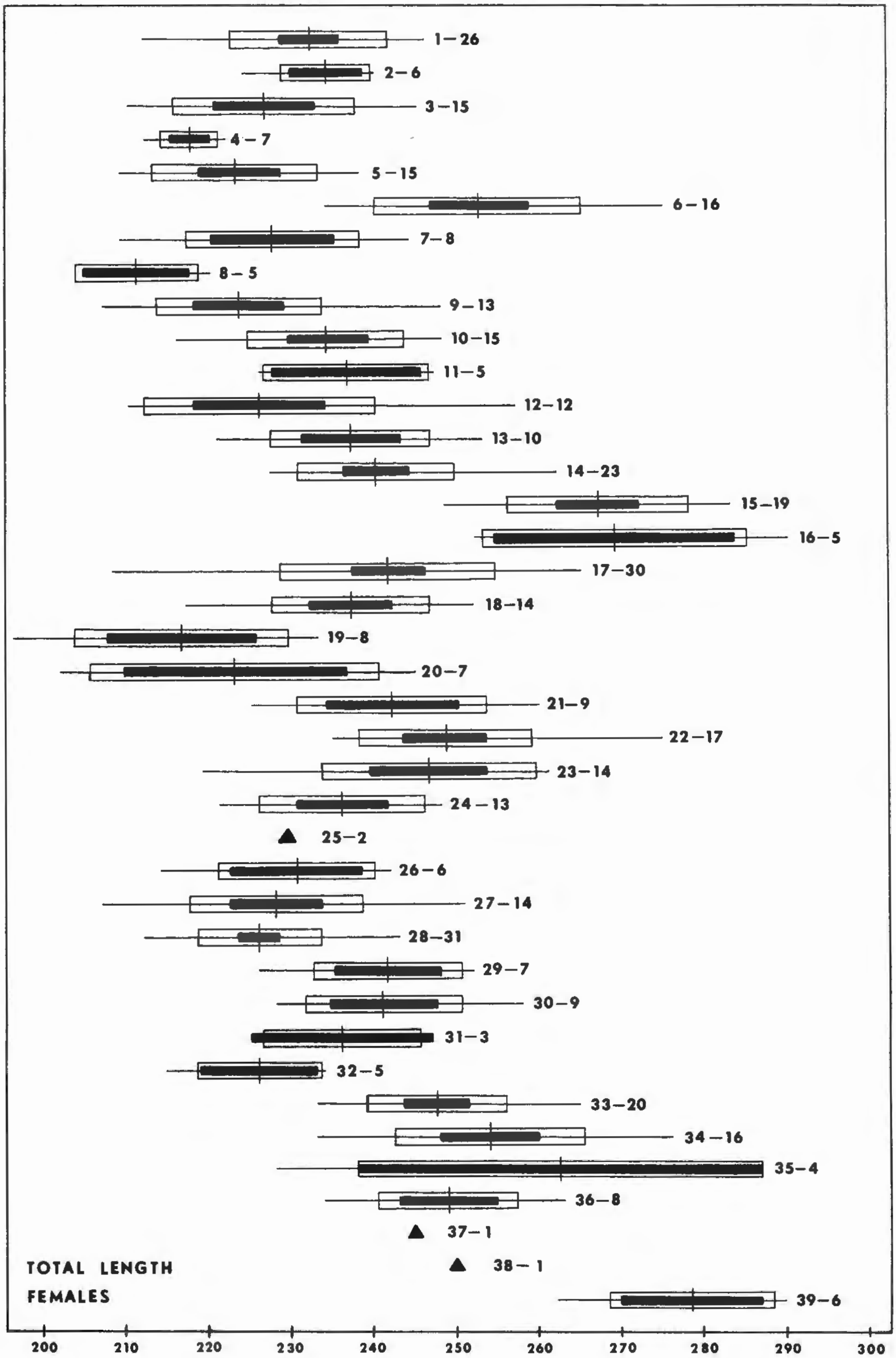


FIG. 9.—Dice grams for four selected measurements of males and females of *Liomys irroratus*. The horizontal line represents the range, vertical line the mean, open rectangle one standard deviation, and closed rectangle two standard errors of the mean. The first number to the right of the grams is the sample number, the second is the sample size. See Fig. 8 and text for key to samples.



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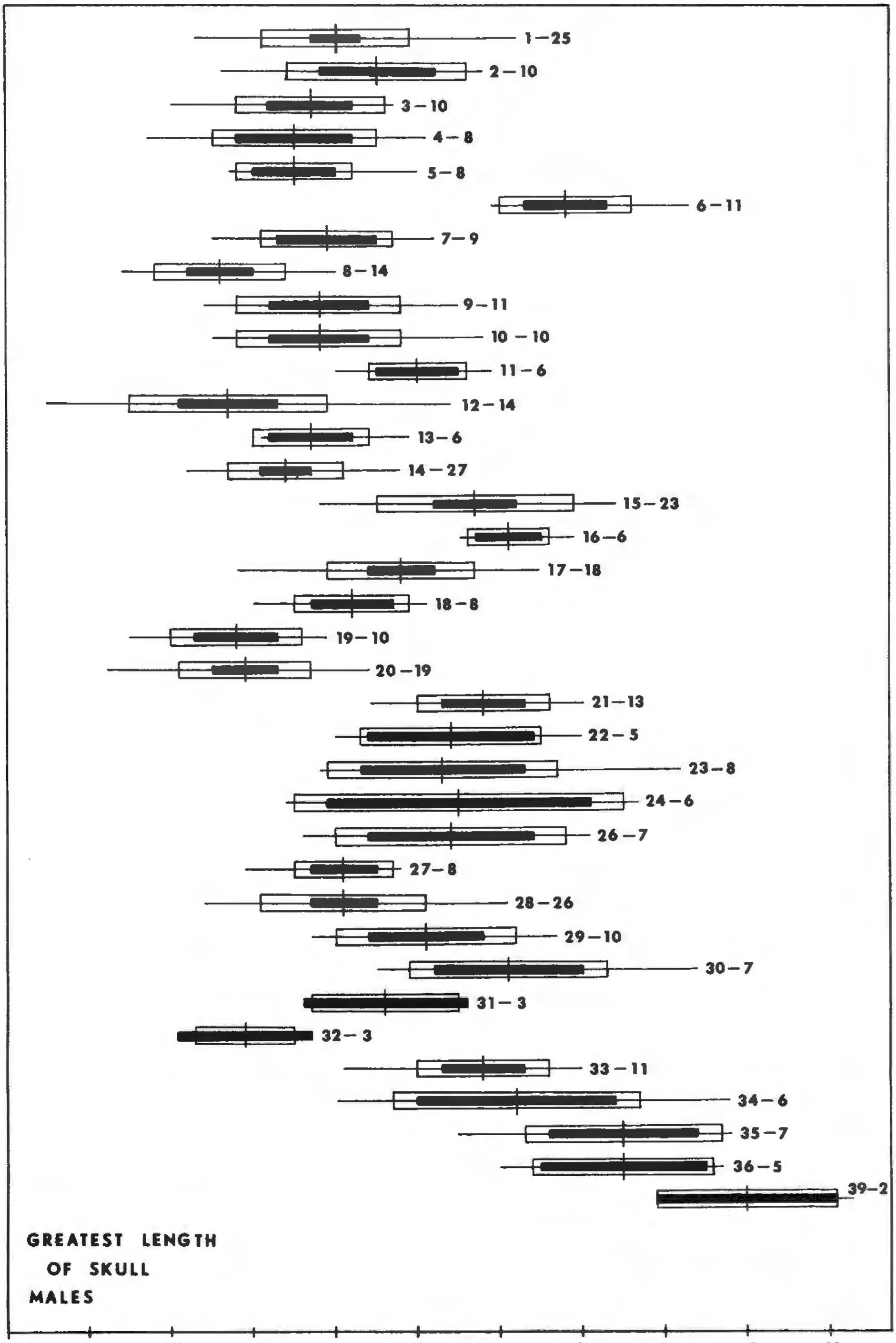

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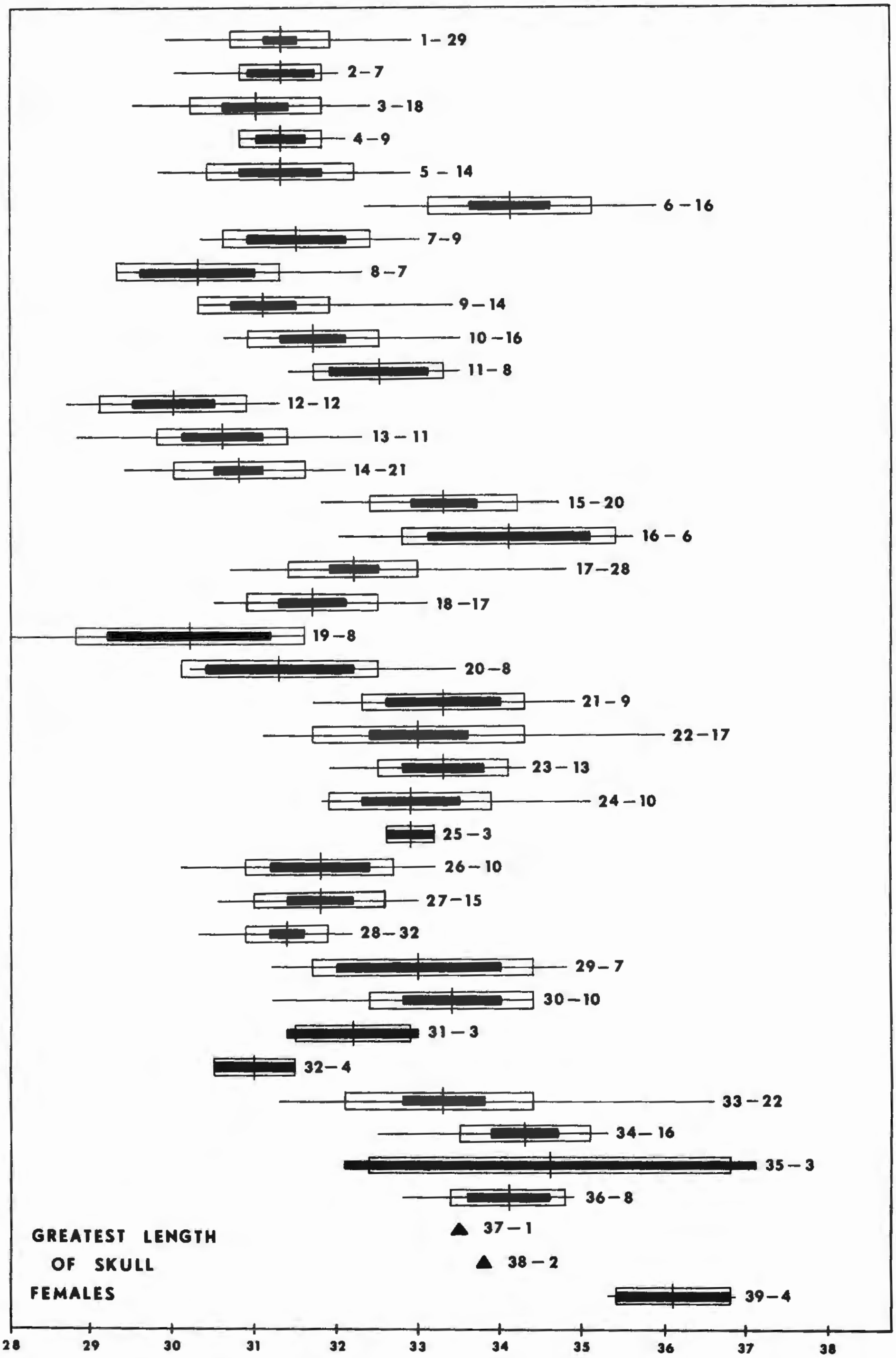

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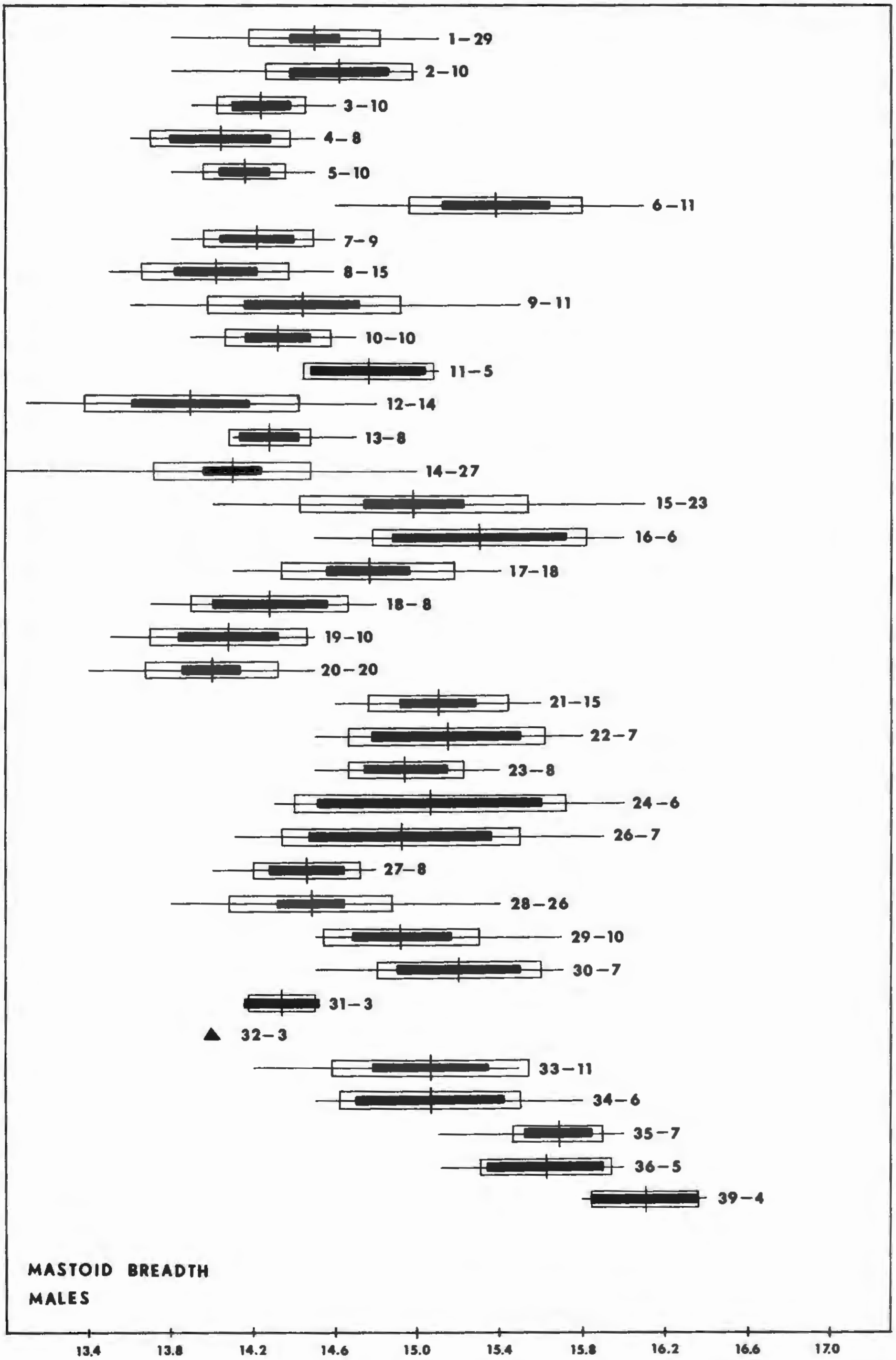

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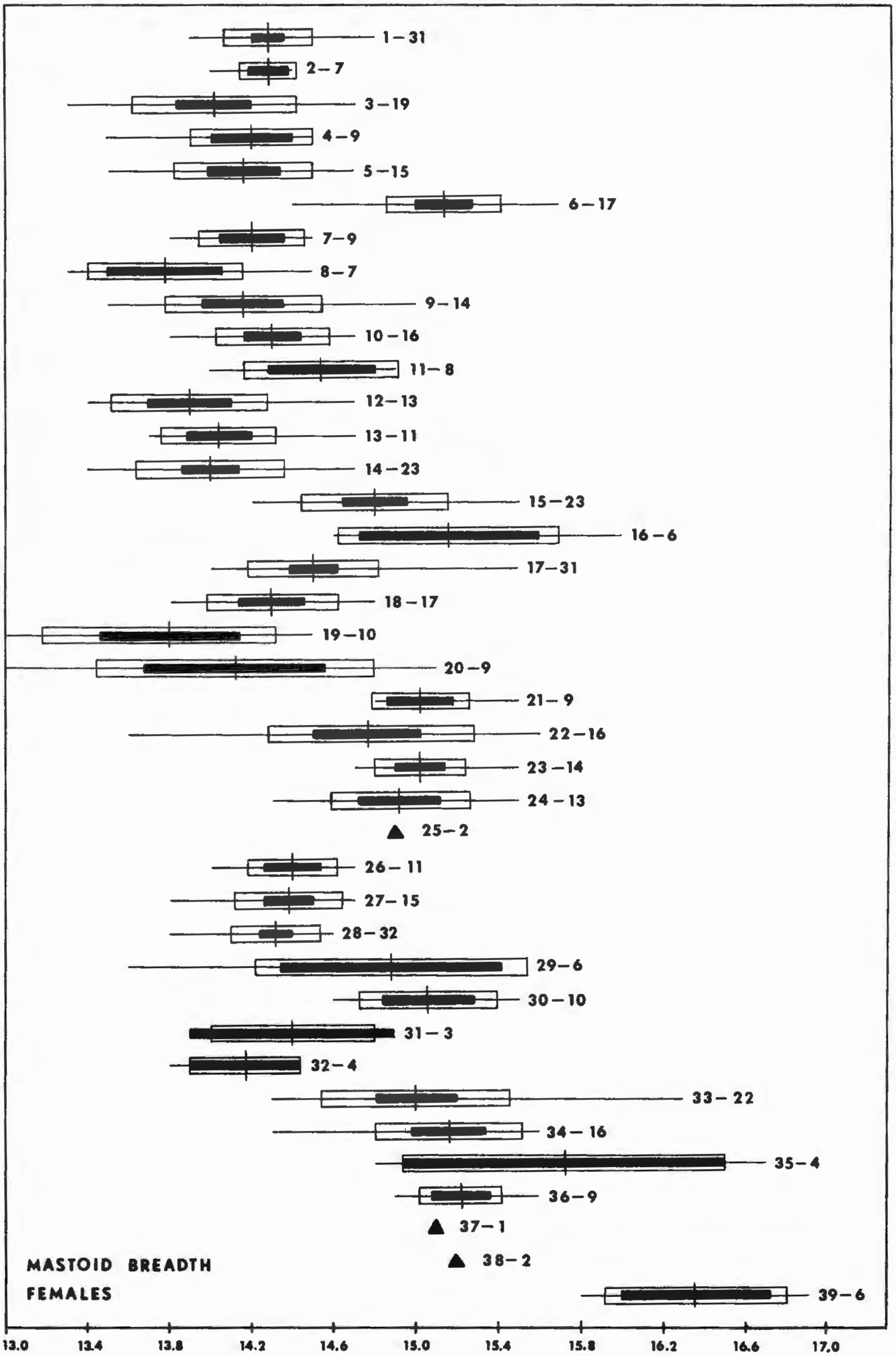

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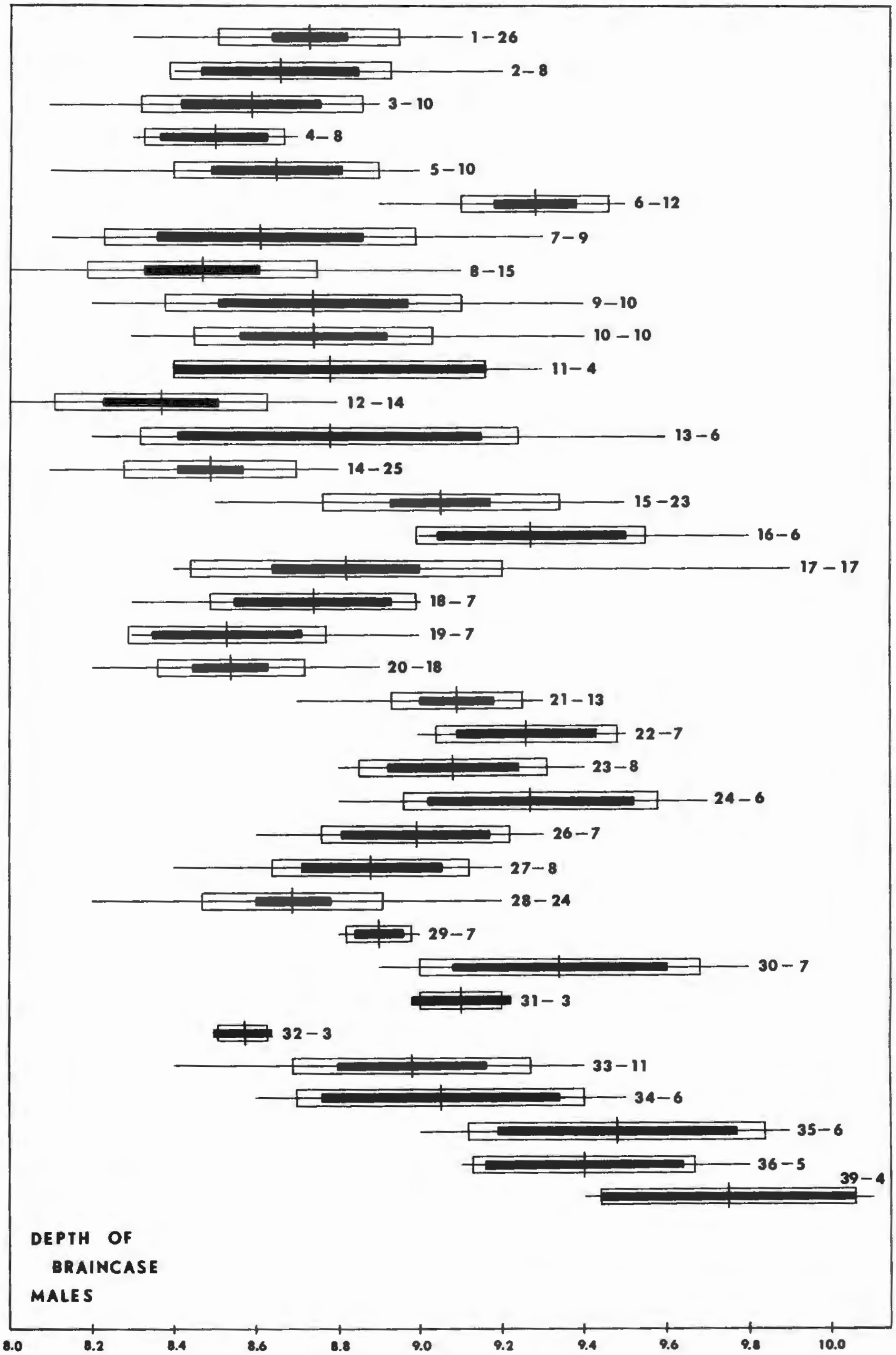

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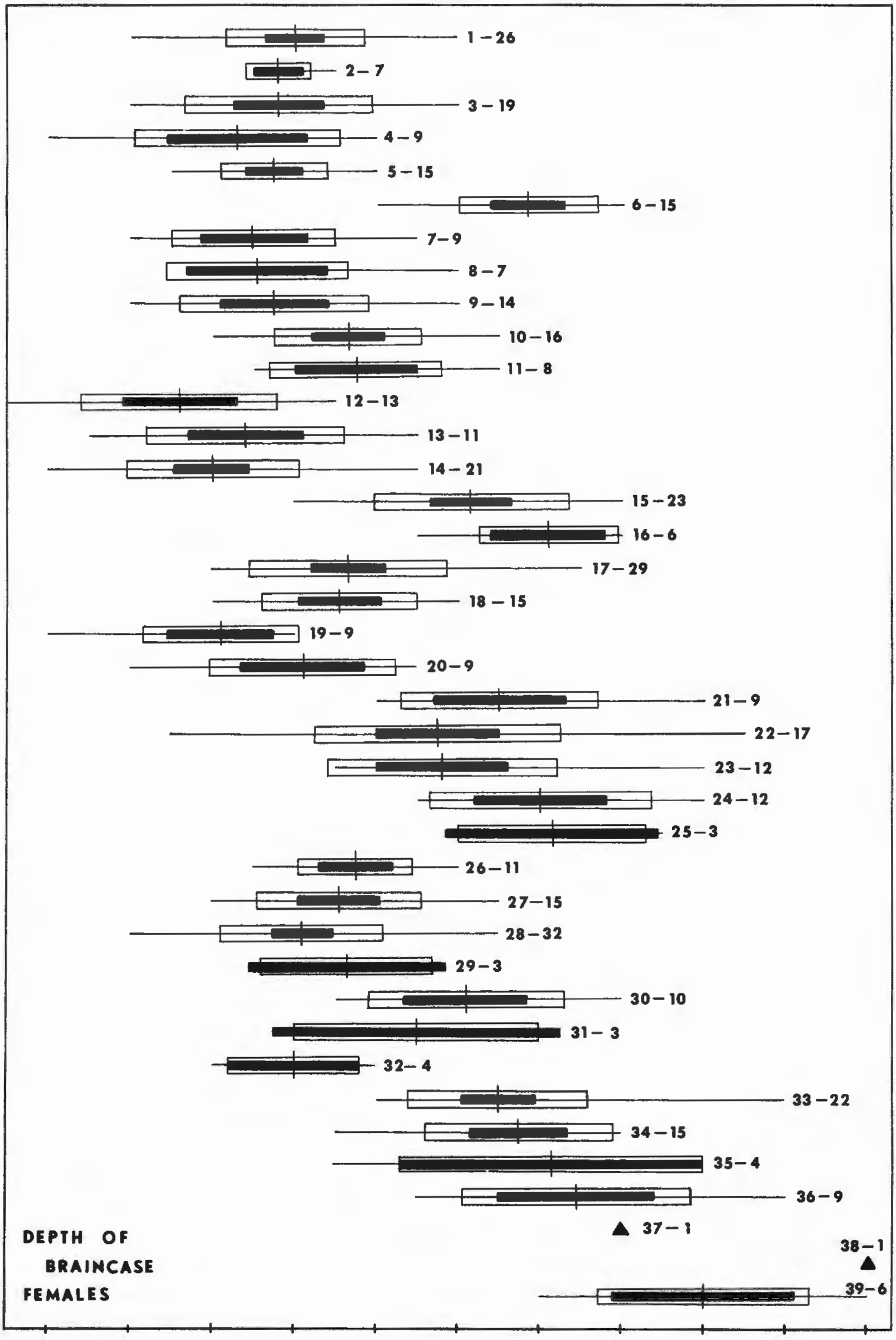


FIG. 9.—Continued.

TABLE 3.—*Geographic variation in external and cranial measurements among 39 samples of* Liomys irroratus. *See text for key to sample numbers.*

Sample	Males				Females			
number	N	Mean	Range	2 SE	N	Mean	Range	2 SE
				Total length				
1	29	241.6	226.0-260.0	3.96	26	231.8	212.0-246.0	3.73
2	8	248.3	227.0-263.0	8.86	6	234.2	224.0-240.0	4.48
3	8	237.6	223.0-254.0	7.72	15	226.7	210.0-245.0	5.76
4	7	226.3	212.0-242.0	9.18	7	217.7	212.0-222.0	2.64
5	9	225.4	209.0-237.0	6.29	15	223.0	209.0-238.0	5.27
6	12	265.9	245.0-280.0	5.45	16	252.7	234.0-275.0	6.24
7	8	230.9	223.0-238.0	4.04	8	227.5	209.0-244.0	7.46
8	10	218.7	208.0-234.0	5.23	5	211.2	205.0-220.0	6.82
9	8	230.9	217.0-242.0	6.62	13	223.5	207.0-248.0	5.67
10	12	240.7	228.0-263.0	5.06	15	233.8	216.0-248.0	5.01
11	4	250.5	245.0-261.0	7.33	5	236.4	226.0-247.0	8.78
12	10	233.5	207.0-253.0	9.07	12	225.8	210.0-257.0	8.06
13	9	247.3	230.0-270.0	8.66	10	236.8	221.0-253.0	5.98
14	22	245.8	223.0-275.0	5.41	23	240.1	227.0-262.0	3.96
15	21	269.3	232.0-296.0	7.70	19	267.1	248.0-283.0	5.10
16	7	270.4	251.0-300.0	15.84	5	268.8	252.0-290.0	14.50
17	16	256.5	225.0-285.0	6.52	30	241.7	208.0-265.0	4.73
18	8	240.8	224.0-269.0	9.89	14	237.0	217.0-252.0	5.05
19	6	231.0	209.0-263.0	15.29	8	216.6	194.0-233.0	9.20
20	16	223.9	195.0-251.0	9.51	7	223.1	202.0-245.0	13.27
21	17	258.1	235.0-293.0	6.84	9	242.1	225.0-260.0	7.76
22	7	255.6	240.0-269.0	7.30	17	248.6	235.0-275.0	5.11
23	7	245.1	225.0-270.0	12.47	14	246.3	219.0-261.0	6.82
24	7	246.9	225.0-267.0	13.33	13	235.8	221.0-248.0	5.50
25					2	229.5	223.0-236.0	13.00
26	4	261.3	247.0-272.0	10.69	6	230.7	214.0-242.0	7.83
27	8	233.4	212.0-250.0	9.16	14	227.8	207.0-251.0	5.52
28	26	234.6	213.0-262.0	5.01	31	226.2	212.0-243.0	2.74
29	9	248.3	235.0-260.0	5.79	7	241.4	226.0-252.0	6.75
30	7	255.1	242.0-269.0	6.27	9	241.1	228.0-258.0	6.40
31	4	247.8	232.0-263.0	13.07	3	236.0	226.0-245.0	11.02
32	3	235.3	229.0-239.0	6.36	5	225.8	215.0-234.0	6.88
33	8	256.3	244.0-280.0	7.90	20	247.3	233.0-265.0	3.86
34	5	254.6	248.0-260.0	3.83	16	254.1	233.0-276.0	5.86
35	6	269.2	260.0-279.0	6.74	4	262.3	228.0-285.0	24.54
36	5	266.4	257.0-276.0	6.09	8	249.0	234.0-263.0	6.07
37					1	245.0		
38					1	250.0		
39	3	292.0	281.0-300.0	11.37	6	278.7	262.0-290.0	8.29
				Length of tail				
1	29	123.2	110.0-136.0	3.15	25	117.5	100.0-129.0	2.75
2	8	131.9	119.0-142.0	5.24	6	120.7	102.0-127.0	7.60
3	8	121.8	110.0-132.0	5.33	15	117.4	104.0-126.0	3.97
4	7	119.7	108.0-132.0	5.52	7	113.7	105.0-120.0	3.64

TABLE 3.—*Continued.*

5	9	112.8	96.0-125.0	6.37	16	116.1	101.0-132.0	4.79
6	12	137.7	120.0-148.0	5.79	15	133.7	120.0-149.0	3.84
7	8	118.3	107.0-127.0	4.88	8	117.6	107.0-127.0	5.04
8	10	109.0	96.0-118.0	3.88	5	106.2	100.0-112.0	4.40
9	8	117.0	106.0-127.0	4.66	13	113.5	102.0-130.0	4.19
10	12	125.9	112.0-145.0	5.04	15	122.0	107.0-132.0	4.23
11	4	133.0	129.0-141.0	5.48	5	129.8	127.0-134.0	2.64
12	11	119.8	103.0-140.0	6.51	12	116.4	105.0-137.0	5.38
13	9	134.9	121.0-152.0	7.19	10	126.8	117.0-135.0	3.36
14	22	137.5	121.0-150.0	3.39	23	131.6	118.0-153.0	3.56
15	21	144.4	117.0-169.0	5.47	20	145.0	133.0-157.0	3.52
16	7	141.3	129.0-158.0	8.66	5	148.0	134.0-163.0	11.44
17	16	129.8	120.0-140.0	3.46	30	125.0	108.0-140.0	2.88
18	8	126.3	111.0-141.0	7.78	14	124.9	110.0-140.0	4.07
19	6	120.7	99.0-142.0	12.84	9	110.4	101.0-115.0	3.30
20	16	115.3	95.0-140.0	6.62	8	118.4	104.0-133.0	7.55
21	17	131.9	116.0-147.0	3.86	9	127.9	115.0-132.0	3.66
22	7	132.9	125.0-145.0	5.55	17	131.2	121.0-151.0	3.58
23	7	125.9	103.0-144.0	10.97	14	128.6	113.0-147.0	6.26
24	7	121.3	110.0-130.0	7.31	13	117.9	105.0-129.0	4.02
25					2	110.0	110.0	0.00
26	4	132.8	126.0-140.0	6.08	6	115.0	108.0-124.0	4.44
27	8	118.8	106.0-132.0	7.05	14	114.0	101.0-131.0	3.64
28	26	117.6	103.0-138.0	3.45	31	112.2	102.0-121.0	1.78
29	9	123.1	116.0-128.0	2.84	7	121.3	109.0-132.0	5.32
30	7	130.7	118.0-139.0	5.07	9	124.1	112.0-136.0	5.07
31	4	128.5	114.0-141.0	11.45	3	128.3	120.0-137.0	9.82
32	3	123.0	114.0-130.0	9.45	5	115.8	110.0-125.0	5.19
33	8	132.1	125.0-146.0	4.67	20	127.3	116.0-139.0	2.68
34	5	127.8	120.0-135.0	5.56	16	129.9	118.0-146.0	4.47
35	6	136.3	127.0-149.0	7.41	4	137.0	117.0-151.0	14.33
36	5	134.2	127.0-140.0	5.53	8	125.3	115.0-134.0	5.89
37					1	127.0		
38					1	128.0		
39	3	144.0	140.0-150.0	6.11	6	138.0	128.0-150.0	6.85
			Length of hind foot					
1	27	28.9	28.0-32.0	0.41	29	28.9	27.0-31.0	0.41
2	9	30.2	28.0-32.0	0.93	7	28.7	28.0-30.0	0.57
3	9	28.7	27.5-30.0	0.60	14	28.3	27.0-32.0	0.75
4	8	28.8	27.5-30.0	0.75	8	28.5	28.0-29.0	0.38
5	10	28.1	26.0-30.0	0.76	16	28.0	26.0-30.0	0.68
6	13	32.4	31.0-34.0	0.57	16	31.5	29.0-34.0	0.70
7	9	29.7	25.5-33.0	1.44	10	29.1	26.0-31.0	0.92
8	12	27.2	25.0-29.0	0.65	6	28.0	27.0-29.0	0.52
9	10	28.5	27.0-30.0	0.64	14	28.1	27.0-31.0	0.68
10	12	30.8	28.0-34.0	0.96	16	30.5	28.0-33.0	0.72
11	6	28.3	27.0-30.0	0.99	4	29.3	29.0-30.0	0.50
12	14	27.7	26.0-30.0	0.64	14	27.3	24.0-29.0	0.69
13	9	29.1	27.0-30.0	0.65	11	28.4	27.0-30.0	0.66
14	24	28.3	26.0-32.0	0.46	24	28.0	26.0-30.0	0.41
15	22	32.6	30.0-35.0	0.73	21	31.8	29.0-35.0	0.63

TABLE 3.—*Continued.*

16	7	34.3	32.0-36.0	1.04	7	32.0	31.0-34.0	0.76
17	21	29.0	27.0-31.0	0.55	32	28.3	25.0-31.0	0.53
18	8	29.6	28.0-31.0	0.92	18	29.2	25.0-32.0	0.82
19	8	27.0	25.0-29.0	1.13	9	26.0	23.0-27.0	1.05
20	16	26.8	23.0-31.0	1.37	8	26.8	22.0-29.0	1.72
21	15	30.4	27.0-34.0	0.92	10	30.3	28.0-32.0	0.85
22	7	31.4	30.0-32.0	0.74	16	30.8	29.0-33.0	0.69
23	8	29.9	28.0-33.0	1.16	14	29.8	28.0-32.0	0.62
24	7	31.0	29.0-34.0	1.57	13	30.3	29.0-33.0	0.76
25					3	30.3	30.0-31.0	0.67
26	5	31.0	29.5-32.0	0.95	7	28.6	26.0-30.0	0.99
27	8	29.1	28.0-30.0	0.59	15	28.6	25.0-30.0	0.68
28	26	28.7	26.5-31.0	0.54	34	28.0	27.0-29.0	0.23
29	9	30.3	29.0-32.0	0.88	7	29.3	25.0-32.0	1.67
30	7	32.1	31.5-33.0	0.36	11	31.1	30.0-32.5	0.54
31	4	30.0	29.0-31.0	1.15	3	28.7	28.0-29.0	0.67
32	3	28.0	28.0		5	28.5	27.5-30.0	0.89
33	12	31.8	29.5-34.0	0.69	23	31.2	29.0-33.0	0.44
34	6	32.2	31.0-33.0	0.61	18	31.3	26.0-34.0	0.77
35	7	33.2	32.0-35.0	0.75	4	32.4	30.5-33.0	1.25
36	5	32.5	29.0-34.5	1.95	9	33.1	32.0-34.0	0.55
37					1	27.0		
38					1	32.0		
39	4	35.0	34.0-37.0	1.35	6	34.1	32.0-35.5	1.11
				Greatest length of skull				
1	25	32.0	30.3-34.2	0.35	29	31.3	29.9-32.9	0.24
2	10	32.5	30.6-33.8	0.72	7	31.3	30.5-32.0	0.37
3	10	31.7	30.0-32.7	0.55	18	31.0	29.5-32.4	0.36
4	8	31.5	29.7-33.1	0.69	9	31.3	30.8-32.1	0.30
5	8	31.5	30.7-33.0	0.49	14	31.3	29.8-32.9	0.48
6	11	34.8	33.9-36.3	0.48	16	34.1	32.3-35.9	0.48
7	9	31.9	30.5-33.2	0.55	9	31.5	30.3-33.0	0.59
8	14	30.6	29.4-32.0	0.42	7	30.3	29.3-32.3	0.75
9	11	31.8	30.4-33.5	0.60	14	31.1	30.3-33.4	0.41
10	10	31.8	30.5-33.8	0.61	16	31.7	30.6-33.5	0.42
11	6	33.0	32.0-33.9	0.53	8	32.5	31.4-33.5	0.56
12	14	30.7	28.5-33.4	0.64	12	30.0	28.7-31.3	0.54
13	6	31.7	31.1-32.9	0.54	11	30.6	28.8-32.3	0.51
14	27	31.4	30.2-32.8	0.26	21	30.8	29.4-32.1	0.33
15	23	33.7	31.8-35.4	0.49	20	33.3	31.8-34.7	0.41
16	6	34.1	33.5-34.9	0.42	6	34.1	32.0-35.6	1.03
17	18	32.8	30.8-34.5	0.44	28	32.2	30.7-34.8	0.33
18	8	32.2	31.0-33.1	0.46	17	31.7	30.5-33.1	0.38
19	10	30.8	29.5-31.9	0.51	8	30.2	27.3-31.5	0.99
20	19	30.9	29.2-32.4	0.38	8	31.3	30.2-33.4	0.87
21	13	33.8	32.4-35.0	0.46	9	33.3	31.7-34.9	0.68
22	5	33.4	32.0-35.0	0.96	17	33.0	31.1-36.0	0.64
23	8	33.3	31.8-36.2	0.96	13	33.3	31.9-34.3	0.46
24	6	33.5	31.4-35.7	1.60	10	32.9	31.8-35.1	0.62
25					3	32.9	32.6-33.2	0.35
26	7	33.4	31.6-35.1	1.06	10	31.8	30.1-33.2	0.56

TABLE 3.—*Continued.*

27	8	32.1	30.9-32.8	0.42	15	31.8	30.5-33.0	0.39
28	26	32.1	30.4-34.1	0.41	32	31.4	30.3-32.2	0.17
29	10	33.1	31.7-34.7	0.69	7	33.0	31.2-34.8	0.98
30	7	34.1	32.5-36.4	0.88	10	33.4	31.2-34.4	0.62
31	3	32.6	31.5-33.3	1.09	3	32.2	31.4-32.8	0.82
32	3	30.9	30.3-31.6	0.76	4	31.0	30.4-31.5	0.49
33	11	33.8	32.1-35.0	0.51	22	33.3	31.3-36.6	0.48
34	6	34.2	32.0-36.8	1.26	16	34.3	32.5-35.3	0.40
35	7	35.5	33.5-36.8	0.90	3	34.6	32.2-36.4	0.25
36	5	35.5	34.0-36.7	0.97	8	34.1	32.8-34.9	0.53
37					1	33.5		
38					2	33.8	33.5-34.1	0.60
39	4	37.0	36.0-38.3	1.08	4	36.1	35.3-36.9	0.68
				Zygomatic breadth				
1	19	15.7	14.5-16.8	0.28	22	15.2	14.5-16.4	0.19
2	5	15.7	14.8-16.3	0.62	6	15.2	14.7-15.8	0.32
3	8	15.1	14.2-16.0	0.36	10	14.6	14.1-15.1	0.21
4	8	14.8	14.3-15.5	0.39	9	14.8	14.2-15.5	0.25
5	9	15.1	14.8-15.6	0.18	12	14.9	14.4-15.4	0.20
6	12	16.4	15.8-16.9	0.21	12	16.1	15.5-16.7	0.21
7	7	14.8	14.4-15.3	0.25	8	14.9	14.1-15.4	0.30
8	14	14.5	13.7-15.8	0.33	6	14.3	15.4-16.0	0.48
9	12	15.3	14.4-15.9	0.22	13	14.7	14.2-15.4	0.22
10	7	15.0	14.1-15.9	0.46	12	15.0	14.4-15.4	0.20
11	5	15.7	15.3-16.1	0.34	7	15.4	14.7-16.2	0.47
12	11	14.4	13.3-15.6	0.45	11	14.6	13.9-15.2	0.24
13	7	15.0	14.5-15.5	0.30	9	14.4	14.1-15.2	0.22
14	21	14.5	14.0-15.4	0.18	19	14.3	13.9-15.0	0.14
15	22	15.9	14.6-17.2	0.31	18	15.8	15.0-17.0	0.26
16	6	16.3	15.7-16.8	0.36	5	16.0	15.4-16.7	0.43
17	9	15.4	14.6-16.2	0.38	17	15.4	14.4-16.4	0.23
18	7	15.4	14.9-15.9	0.32	14	15.2	14.2-15.8	0.21
19	5	14.6	14.2-15.2	0.39	5	14.4	13.8-14.8	0.33
20	19	14.4	13.7-15.1	0.23	5	14.4	13.5-15.2	0.64
21	13	16.1	15.4-16.8	0.23	5	15.7	14.9-16.4	0.50
22	7	15.8	14.7-16.9	0.52	13	15.5	14.3-16.6	0.38
23	7	15.8	14.8-16.5	0.42	8	15.9	15.3-16.6	0.29
24	6	16.3	15.1-17.7	1.06	12	16.0	14.8-17.0	0.34
25					3	16.0	15.7-16.2	0.29
26	4	16.3	15.6-16.9	0.65	7	15.6	14.9-16.4	0.38
27	5	15.3	14.9-15.9	0.42	10	15.2	14.6-15.7	0.24
28	21	15.6	14.8-16.6	0.25	28	15.3	14.6-16.3	0.15
29	9	16.0	15.2-17.3	0.43	3	16.3	14.7-17.5	1.65
30	7	16.1	14.9-16.8	0.50	8	16.2	15.0-16.8	0.40
31	2	15.1	14.6-15.5	0.90	3	15.4	15.1-15.9	0.50
32	2	14.6	14.5-14.6	0.10	3	14.8	14.3-15.2	0.53
33	12	16.0	15.0-16.5	0.30	18	16.0	15.4-17.5	0.27
34	5	16.2	15.6-17.3	0.57	13	16.2	15.1-17.2	0.38
35	5	16.7	15.8-17.0	0.46	4	16.6	15.7-17.4	0.75
36	4	17.1	15.7-18.0	0.99	6	16.7	16.1-17.7	0.48
37					1	16.2		

TABLE 3.—*Continued.*

38					1	16.7		
39	3	17.5	17.3-17.8	0.29	4	17.1	16.2-17.8	0.73
				Interorbital constriction				
1	31	8.3	7.8-9.2	0.12	32	8.0	7.6-8.7	0.10
2	10	8.3	7.8-8.6	0.19	7	8.0	7.7-8.6	0.24
3	11	7.8	7.4-8.2	0.14	19	7.6	7.0-8.1	0.13
4	8	7.8	7.4-8.4	0.22	9	7.8	7.5-8.2	0.17
5	10	7.9	7.5-8.3	0.17	16	7.8	7.4-8.3	0.10
6	13	8.2	7.7-9.1	0.21	19	8.2	7.7-8.8	0.15
7	9	7.5	7.2-7.6	0.85	10	7.5	7.2-8.0	0.16
8	17	7.5	7.1-8.0	0.12	8	7.3	6.6-8.0	0.29
9	12	7.8	7.2-8.4	0.21	15	7.7	7.3-8.2	0.15
10	12	7.5	7.0-8.2	0.21	16	7.5	7.0-8.0	0.14
11	7	8.1	7.0-8.7	0.43	10	8.1	7.6-8.4	0.16
12	14	7.5	7.1-8.1	0.18	14	7.4	6.6-7.7	0.17
13	9	7.7	7.3-8.0	0.16	11	7.5	6.7-8.0	0.24
14	28	7.7	7.3-8.2	0.09	28	7.9	7.0-8.4	0.12
15	25	8.2	7.5-8.6	0.13	26	8.1	7.5-9.0	0.14
16	6	8.3	8.1-8.7	0.19	7	8.4	8.0-8.8	0.20
17	19	7.9	7.3-8.6	0.18	32	7.7	7.0-8.6	0.12
18	8	7.7	7.3-8.0	0.17	18	7.7	7.0-8.2	0.14
19	10	7.3	6.8-7.8	0.24	9	7.5	6.9-7.9	0.23
20	20	7.5	6.7-8.0	0.13	9	7.4	6.9-8.0	0.27
21	17	8.5	8.0-8.9	0.12	11	8.4	8.0-9.0	0.21
22	8	8.3	7.9-8.7	0.18	17	8.2	7.8-8.6	0.12
23	8	8.2	8.0-8.4	0.11	14	8.2	7.5-8.7	0.17
24	6	8.1	7.5-8.6	0.36	13	7.9	7.3-8.4	0.16
25					3	7.9	7.4-8.4	0.58
26	8	8.4	7.8-9.0	0.32	11	8.2	7.6-8.6	0.20
27	8	8.1	7.7-8.5	0.19	14	7.8	7.3-8.2	0.14
28	27	7.9	7.2-8.7	0.13	34	7.7	7.2-8.3	0.10
29	10	8.2	7.8-8.7	0.18	7	8.2	7.2-8.6	0.36
30	6	8.5	8.2-8.8	0.23	11	8.2	7.8-8.7	0.17
31	3	8.2	8.0-8.5	0.29	3	7.1	5.6-8.0	1.54
32	3	7.7	7.4-7.9	0.29	5	7.5	7.3-7.8	0.17
33	12	8.3	7.9-8.7	0.17	23	8.3	7.5-9.3	0.21
34	6	8.5	8.0-9.0	0.28	18	8.6	8.2-9.4	0.15
35	7	8.9	8.6-9.2	0.16	4	8.8	8.2-9.0	0.39
36	4	9.1	8.7-9.5	0.33	8	8.5	8.2-9.1	0.21
37					1	8.2		
38					2	8.7	8.6-8.7	0.10
39	4	9.2	8.6-9.8	0.49	5	8.9	8.4-9.3	0.32
				Mastoid breadth				
1	29	14.5	13.8-15.1	0.12	31	14.3	13.9-14.8	0.77
2	10	14.6	13.8-15.0	0.23	7	14.3	14.0-14.4	0.10
3	10	14.2	13.9-14.6	0.14	19	14.0	13.3-14.7	0.17
4	8	14.0	13.6-14.5	0.24	9	14.2	13.5-14.5	0.20
5	10	14.2	13.8-14.5	0.12	15	14.2	13.5-14.7	0.17
6	11	15.4	14.6-16.1	0.26	17	15.1	14.6-15.7	0.14
7	9	14.2	13.8-14.6	0.18	9	14.2	13.8-14.5	0.17
8	15	14.0	13.5-14.6	0.19	7	13.8	13.3-14.5	0.28

TABLE 3.—*Continued.*

9	11	14.4	13.6-15.5	0.29	14	14.2	13.5-15.0	0.20
10	10	14.3	13.9-14.7	0.16	16	14.3	13.8-14.7	0.14
11	5	14.8	14.5-15.1	0.28	8	14.5	14.0-14.9	0.26
12	14	13.9	13.1-14.8	0.27	13	13.9	13.4-14.7	0.21
13	8	14.3	14.1-14.7	0.14	11	14.0	13.7-14.7	0.16
14	27	14.1	13.0-14.9	0.15	23	14.0	13.4-14.7	0.15
15	23	15.0	13.9-16.1	0.23	23	14.8	14.2-15.5	0.15
16	6	15.3	14.5-16.0	0.43	6	15.2	14.6-16.0	0.45
17	18	14.8	13.9-15.4	0.20	31	14.5	14.0-15.5	0.12
18	8	14.3	13.7-14.8	0.27	17	14.3	13.8-14.8	0.15
19	10	14.1	13.5-14.5	0.24	10	13.8	13.0-14.5	0.33
20	20	14.0	13.4-14.5	0.14	9	14.1	13.0-15.1	0.45
21	15	15.1	14.6-15.6	0.17	9	15.0	14.8-15.5	0.16
22	7	15.1	14.5-15.8	0.36	16	14.8	13.6-15.6	0.26
23	8	14.9	14.5-15.4	0.20	14	15.0	14.7-15.5	0.12
24	6	15.1	14.3-16.0	0.54	13	14.9	14.3-15.5	0.19
25					2	14.9	14.7-15.1	0.40
26	7	14.9	14.1-15.9	0.43	11	14.4	14.0-14.7	0.13
27	8	14.5	14.0-14.8	0.18	15	14.4	13.8-14.7	0.13
28	26	14.5	13.8-15.4	0.15	32	14.3	13.8-14.6	0.08
29	10	14.9	14.5-15.7	0.24	6	14.9	13.6-15.4	0.54
30	7	15.2	14.5-15.7	0.31	10	15.1	14.6-15.5	0.21
31	3	14.3	14.2-14.5	0.18	3	14.4	14.0-14.8	0.46
32	3	14.0	14.0		4	14.1	13.8-14.3	0.22
33	11	15.1	14.2-15.5	0.28	22	15.0	14.3-16.3	0.20
34	6	15.1	14.5-15.8	0.36	16	15.2	14.3-15.6	0.18
35	7	15.7	15.3-16.0	0.17	4	15.7	14.8-16.7	0.78
36	5	15.6	15.3-16.0	0.28	9	15.2	14.9-15.6	0.13
37					1	15.1		
38					2	15.2	14.8-15.5	0.70
39	4	16.1	15.8-16.4	0.26	6	16.4	15.8-16.9	0.36
				Length of nasals				
1	31	12.9	12.0-14.0	0.18	31	12.5	11.8-13.3	0.14
2	10	13.2	12.0-14.1	0.43	7	12.5	12.0-13.1	0.30
3	11	12.7	11.9-13.4	0.29	18	12.5	11.3-13.2	0.21
4	8	12.4	11.9-12.9	0.23	9	12.4	12.1-12.7	0.13
5	7	12.4	11.8-13.2	0.32	12	12.3	11.2-13.4	0.40
6	12	13.8	12.9-15.0	0.40	18	13.3	12.4-14.4	0.26
7	9	12.4	10.8-13.2	0.49	10	12.3	11.5-13.4	0.37
8	16	12.0	11.2-12.7	0.23	8	11.8	11.2-12.8	0.33
9	12	12.5	11.1-13.2	0.31	14	12.1	11.1-13.3	0.29
10	12	12.4	11.5-13.5	0.40	16	12.3	11.2-12.9	0.23
11	7	13.1	12.8-13.7	0.31	10	12.7	12.0-13.8	0.40
12	14	11.7	10.6-12.7	0.32	13	11.4	10.6-12.2	0.26
13	9	12.1	11.1-13.5	0.46	11	11.6	10.9-12.2	0.22
14	28	12.3	11.4-13.4	0.17	29	11.9	11.3-12.7	0.15
15	24	13.1	12.0-14.0	0.22	25	13.0	12.0-14.2	0.22
16	7	13.2	12.6-14.1	0.39	7	13.3	12.1-13.8	0.44
17	22	12.6	11.4-13.5	0.24	31	12.3	10.9-14.2	0.23
18	8	12.7	12.0-13.2	0.30	18	12.2	11.2-13.0	0.22
19	10	11.6	11.0-12.6	0.31	9	11.4	9.9-12.7	0.66

TABLE 3.—*Continued.*

20	20	11.8	10.8-12.7	0.23	8	11.9	11.3-13.5	0.55
21	17	13.4	12.2-14.2	0.26	11	13.2	12.3-14.6	0.42
22	8	13.3	12.7-14.0	0.33	14	13.0	12.2-14.8	0.35
23	8	13.3	12.4-15.1	0.64	14	13.0	12.1-13.8	0.32
24	6	13.4	12.0-15.1	1.14	12	12.8	11.5-14.3	0.40
25					3	12.6	12.3-13.0	0.42
26	8	12.6	11.6-13.3	0.46	11	12.0	11.0-13.0	0.36
27	7	12.2	11.4-13.0	0.38	14	12.4	11.2-13.4	0.39
28	27	12.4	11.4-13.4	0.25	35	12.2	11.0-13.5	0.18
29	10	13.2	12.2-13.9	0.39	6	13.1	12.1-14.1	0.66
30	7	13.7	13.0-15.2	0.58	11	13.0	12.3-13.9	0.33
31	3	12.7	12.0-13.3	0.77	4	12.6	12.2-12.8	0.31
32	3	11.8	11.6-12.1	0.33	5	11.9	11.5-12.4	0.32
33	12	13.1	12.0-13.7	0.27	23	12.9	12.0-14.2	0.26
34	6	13.5	12.4-14.5	0.61	16	13.5	12.4-14.2	0.28
35	7	13.8	12.7-14.7	0.55	3	14.0	13.5-14.5	0.58
36	5	13.8	12.7-14.4	0.61	9	13.2	12.3-15.8	0.34
37					1	14.1		
38					2	13.3	13.2-13.4	0.20
39	4	14.8	14.1-15.9	0.79	3	14.1	13.7-14.3	0.37
				Length of rostrum				
1	27	14.0	13.0-15.2	0.18	29	13.5	12.7-14.4	0.14
2	7	14.2	13.3-14.9	0.50	7	13.4	13.0-13.9	0.26
3	10	13.8	13.0-14.6	0.31	18	13.4	12.3-14.2	0.24
4	8	13.6	12.7-14.4	0.36	9	13.6	13.2-14.0	0.22
5	7	13.7	13.6-14.2	0.17	12	13.4	12.5-14.2	0.27
6	12	15.5	14.8-16.7	0.34	17	15.1	14.0-16.4	0.29
7	9	13.9	13.2-14.6	0.29	10	13.7	13.0-14.4	0.31
8	15	13.1	12.5-14.2	0.26	8	12.9	12.4-13.9	0.35
9	11	13.7	13.0-14.6	0.31	14	13.4	13.0-14.3	0.20
10	11	14.0	13.1-15.2	0.39	16	13.7	12.9-14.8	0.27
11	7	14.7	14.3-15.3	0.27	10	14.5	13.8-15.3	0.25
12	13	13.6	12.2-14.6	0.35	13	13.2	12.3-13.9	0.31
13	8	14.2	13.5-15.3	0.45	10	13.4	12.9-14.2	0.24
14	27	14.0	12.9-15.0	0.18	29	13.8	12.7-14.6	0.17
15	23	15.2	14.0-16.2	0.27	23	15.0	14.0-16.0	0.25
16	7	15.4	15.0-16.3	0.34	6	15.5	14.7-16.4	0.53
17	22	14.7	13.4-15.5	0.20	29	14.4	13.6-16.0	0.20
18	8	14.3	13.8-14.7	0.22	18	14.2	13.3-14.9	0.24
19	9	13.7	13.1-14.4	0.24	6	12.8	12.0-13.6	0.53
20	18	13.6	12.4-14.7	0.30	6	13.9	13.1-15.0	0.61
21	17	15.3	14.6-16.0	0.22	10	15.0	13.9-15.8	0.36
22	8	14.8	14.0-15.6	0.38	14	14.7	13.5-16.0	0.38
23	8	14.6	13.6-16.9	0.76	14	14.7	14.0-15.4	0.23
24	6	15.3	13.9-16.8	1.08	12	14.7	14.0-15.8	0.34
25					3	14.6	14.5-14.7	0.13
26	8	14.5	12.2-15.7	0.87	11	14.0	13.3-14.7	0.29
27	4	14.5	14.3-14.9	0.27	14	13.9	13.2-14.7	0.26
28	27	14.1	13.2-15.4	0.24	35	13.7	12.9-14.9	0.14
29	7	14.3	13.7-15.2	0.41	4	14.4	13.3-16.1	0.13
30	7	15.0	14.5-16.0	0.38	11	14.6	13.2-15.2	0.42

TABLE 3.—*Continued.*

31	3	14.6	14.1-15.0	0.53	4	13.9	13.2-14.5	0.53
32	3	13.4	13.0-13.9	0.55	5	13.5	12.9-14.0	0.40
33	12	14.9	14.3-15.9	0.29	23	14.6	13.6-16.3	0.25
34	6	15.4	14.2-16.9	0.71	17	15.2	13.6-16.0	0.32
35	7	15.9	15.3-16.8	0.42	3	15.4	14.5-16.0	0.90
36	5	16.0	15.1-16.6	0.53	9	15.1	14.4-15.6	0.27
37					1	15.3		
38					1	15.3		
39	4	17.3	16.3-17.9	0.74	3	16.2	16.0-16.7	0.47
			Length of maxillary toothrow					
1	32	5.0	4.7-5.3	0.06	32	4.9	4.5-5.2	0.07
2	10	5.1	4.6-5.4	0.13	7	4.8	4.2-5.3	0.26
3	10	4.9	4.6-5.3	0.13	19	4.8	4.4-5.1	0.08
4	8	4.7	4.4-5.0	0.13	9	4.7	4.4-5.0	0.11
5	10	4.8	4.6-5.2	0.11	16	4.7	4.3-5.1	0.12
6	13	5.4	5.1-5.7	0.12	18	5.3	5.0-5.9	0.13
7	9	4.8	4.7-5.1	0.11	10	4.8	4.6-5.1	0.11
8	16	4.7	4.4-4.8	0.07	8	4.5	4.3-4.7	0.11
9	12	4.7	4.3-5.2	0.16	15	4.8	4.5-5.2	0.10
10	12	4.8	4.4-5.1	0.14	16	4.8	4.5-5.1	0.08
11	6	4.8	4.6-4.9	0.08	10	4.8	4.4-5.2	0.17
12	14	4.9	4.6-5.3	0.10	14	4.9	4.6-5.2	0.10
13	9	4.9	4.6-5.2	0.12	11	4.8	4.4-5.1	0.14
14	26	4.8	4.4-5.3	0.08	28	4.8	4.4-5.2	0.08
15	25	5.3	4.9-5.9	0.11	25	5.3	4.8-5.9	0.13
16	7	5.6	5.2-6.2	0.27	7	5.5	5.3-5.6	0.08
17	21	5.1	4.5-5.6	0.10	32	5.1	4.5-5.5	0.07
18	8	5.0	4.8-5.3	0.13	17	5.0	4.8-5.2	0.07
19	10	4.9	4.8-5.0	0.06	10	4.7	4.3-5.0	0.16
20	20	5.0	4.5-5.4	0.10	8	5.0	4.6-5.3	0.16
21	17	5.5	5.2-5.8	0.10	11	5.2	4.8-5.7	0.15
22	9	5.3	4.8-5.7	0.20	17	5.2	4.6-5.7	0.15
23	8	5.1	4.9-5.4	0.10	14	5.2	4.7-5.4	0.10
24	6	5.5	5.0-5.9	0.27	13	5.4	5.1-5.8	0.13
25					3	5.3	5.2-5.4	0.13
26	8	5.2	4.8-5.8	0.20	10	5.0	4.9-5.1	0.06
27	8	5.2	4.8-5.3	0.13	16	5.2	4.9-5.5	0.09
28	27	5.1	4.8-5.4	0.06	34	5.0	4.4-5.4	0.07
29	10	5.3	5.0-5.7	0.13	5	5.1	4.5-5.5	0.39
30	7	5.5	5.2-5.7	0.14	11	5.3	4.8-5.7	0.15
31	3	5.3	5.2-5.5	0.20	4	5.2	5.1-5.4	0.13
32	2	5.2	5.1-5.3	0.20	4	5.0	4.8-5.2	0.17
33	12	5.5	5.1-6.0	0.14	23	5.4	4.9-5.9	0.12
34	6	5.4	5.0-5.6	0.19	18	5.4	4.5-6.0	0.16
35	7	5.8	5.4-6.0	0.14	4	5.5	5.0-5.7	0.34
36	5	5.8	5.6-6.0	0.13	10	5.7	5.4-5.9	0.09
37					1	6.0		
38					2	5.9	5.9	
39	4	5.9	5.7-6.0	0.14	6	6.1	5.6-6.7	0.34

TABLE 3.—*Continued.*

				Depth of braincase				
1	26	8.7	8.3-9.1	0.87	26	8.6	8.2-9.0	0.07
2	8	8.7	8.4-9.2	0.19	7	8.6	8.5-8.7	0.06
3	10	8.6	8.1-8.9	0.17	19	8.6	8.1-9.0	0.11
4	8	8.5	8.3-8.7	0.13	9	8.5	8.0-8.8	0.17
5	10	8.7	8.1-9.0	0.16	15	8.6	8.3-8.8	0.07
6	12	9.3	8.9-9.5	0.10	15	9.2	8.8-9.4	0.09
7	9	8.6	8.1-9.3	0.25	9	8.5	8.2-8.9	0.13
8	15	8.5	8.0-9.1	0.14	7	8.5	8.4-9.0	0.17
9	10	8.7	8.2-9.4	0.23	14	8.6	8.2-9.0	0.13
10	10	8.7	8.3-9.4	0.18	16	8.7	8.4-9.1	0.09
11	4	8.8	8.5-9.3	0.38	8	8.8	8.5-9.1	0.15
12	14	8.4	8.0-8.8	0.14	13	8.3	7.9-8.7	0.14
13	6	8.8	8.2-9.6	0.37	11	8.5	8.1-8.9	0.14
14	25	8.5	8.1-8.8	0.08	21	8.4	8.0-8.9	0.09
15	23	9.1	8.5-9.5	0.12	23	9.0	8.6-9.4	0.10
16	6	9.3	9.0-9.8	0.23	6	9.2	8.9-9.4	0.14
17	17	8.8	8.4-9.9	0.18	29	8.7	8.4-9.3	0.09
18	7	8.7	8.3-9.0	0.19	15	8.7	8.4-9.0	0.10
19	7	8.5	8.3-9.0	0.18	9	8.4	8.0-8.6	0.13
20	18	8.5	8.2-8.9	0.09	9	8.6	8.2-8.9	0.15
21	13	9.1	8.7-9.3	0.09	9	9.1	8.8-9.6	0.16
22	7	9.3	9.0-9.5	0.17	17	8.9	8.3-9.7	0.15
23	8	9.1	8.8-9.4	0.16	12	9.0	8.7-9.6	0.16
24	6	9.3	8.8-9.7	0.26	12	9.2	8.9-9.6	0.16
25					3	9.2	9.1-9.5	0.27
26	7	9.0	8.6-9.3	0.18	11	8.8	8.5-9.0	0.09
27	8	8.9	8.4-9.2	0.17	15	8.7	8.4-9.1	0.10
28	24	8.7	8.2-9.2	0.09	32	8.6	8.2-9.1	0.07
29	7	8.9	8.8-9.0	0.06	3	8.7	8.5-8.9	0.24
30	7	9.3	8.9-9.8	0.26	10	9.0	8.7-9.4	0.15
31	3	9.1	9.0-9.2	0.12	3	8.9	8.6-9.2	0.35
32	3	8.6	8.5-8.6	0.07	4	8.6	8.4-8.8	0.16
33	11	9.0	8.4-9.4	0.18	22	9.1	8.8-9.8	0.09
34	6	9.1	8.6-9.5	0.29	15	9.1	8.7-9.4	0.12
35	6	9.5	9.0-9.9	0.29	4	9.2	8.7-9.6	0.38
36	5	9.4	9.1-9.8	0.24	9	9.3	8.9-9.8	0.19
37					1	9.4		
38					1	10.0		
39	4	9.8	9.4-10.1	0.31	6	9.6	9.2-10.0	0.22
				Interparietal width				
1	29	7.5	6.5-8.7	0.22	30	7.2	6.0-8.0	0.17
2	10	7.3	6.2-8.2	0.40	7	6.7	5.8-7.6	0.42
3	10	8.0	7.1-8.6	0.28	19	7.7	7.0-8.7	0.21
4	8	7.8	7.2-8.4	0.28	9	7.8	7.4-8.6	0.26
5	10	8.1	7.0-8.9	0.39	14	7.8	6.9-9.0	0.34
6	12	9.2	8.3-9.7	0.23	18	8.8	8.0-9.6	0.24
7	9	8.4	7.7-8.8	0.24	9	8.4	7.5-9.2	0.36
8	15	8.1	7.4-8.7	0.21	7	7.8	7.4-8.4	0.30
9	11	8.1	7.1-8.8	0.26	13	7.9	6.9-9.0	0.37
10	10	8.6	7.8-9.0	0.25	16	8.6	8.0-9.0	0.17

TABLE 3.—*Continued.*

11	5	8.3	7.8-9.1	0.42	8	8.2	7.6-9.1	0.37
12	14	7.7	7.0-8.3	0.23	13	7.9	7.2-8.7	0.27
13	7	8.2	7.5-8.8	0.35	11	8.2	7.0-9.3	0.37
14	26	8.2	7.5-8.9	0.15	21	8.0	6.7-9.2	0.28
15	23	8.6	7.7-9.5	0.24	24	8.6	7.7-9.7	0.21
16	6	8.5	7.9-8.9	0.32	6	8.1	7.7-8.9	0.36
17	17	8.3	7.4-9.2	0.28	29	8.4	7.2-9.4	0.18
18	8	8.1	7.4-8.9	0.41	15	7.9	7.0-9.0	0.27
19	10	7.8	6.4-8.5	0.41	10	7.6	6.7-8.2	0.29
20	19	7.8	7.2-8.4	0.16	9	7.8	7.1-8.8	0.43
21	13	8.7	8.1-9.3	0.22	9	8.7	8.1-9.7	0.36
22	5	9.2	8.6-9.9	0.42	17	8.6	7.7-9.4	0.25
23	8	8.7	8.2-9.1	0.24	14	8.7	7.9-9.6	0.26
24	5	7.4	6.9-7.8	0.29	13	7.7	6.9-8.9	0.29
25					2	8.1	7.3-8.9	1.60
26	7	8.9	8.4-9.8	0.37	10	8.7	8.4-9.0	0.18
27	8	8.8	8.2-9.4	0.27	16	8.8	8.2-9.5	0.17
28	26	8.6	7.9-9.4	0.15	33	8.4	7.3-9.3	0.15
29	10	8.7	7.7-9.6	0.41	5	8.4	6.2-9.3	1.14
30	7	8.7	8.3-9.1	0.26	9	8.7	7.8-9.2	0.32
31	3	8.5	7.8-9.2	0.81	3	8.6	8.1-8.9	0.48
32	3	8.4	8.2-8.7	0.29	4	8.3	7.8-8.7	0.42
33	11	8.7	7.4-10.4	0.56	22	8.9	7.9-9.6	0.16
34	6	8.8	8.0-9.7	0.50	17	9.0	7.8-9.8	0.26
35	7	9.1	8.7-10.0	0.36	4	9.2	8.4-9.8	0.58
36	5	9.1	8.4-9.7	0.45	10	8.7	8.1-9.3	0.23
37					1	5.4		
38					2	7.7	7.4-8.0	0.60
39	4	8.5	7.9-9.2	0.61	6	8.8	8.2-9.5	0.43
				Interparietal length				
1	29	4.0	3.3-4.5	0.12	31	3.9	3.3-4.5	0.09
2	10	4.0	3.4-4.3	0.15	7	3.7	3.4-4.1	0.21
3	10	4.2	3.5-4.6	0.19	19	4.0	3.5-4.7	0.13
4	8	4.0	3.6-4.2	0.15	9	3.9	3.6-4.3	0.15
5	10	4.0	3.7-4.3	0.14	14	4.0	3.5-4.4	0.12
6	12	4.0	3.5-4.5	0.16	18	3.8	3.4-4.4	0.13
7	9	3.9	3.5-4.4	0.24	9	4.0	3.6-4.3	0.17
8	15	4.2	3.8-4.6	0.11	7	3.8	3.5-4.0	0.17
9	11	4.0	3.0-4.5	0.25	14	4.1	3.7-4.5	0.12
10	10	3.8	3.2-4.2	0.21	16	3.9	3.3-4.4	0.18
11	5	4.1	3.8-4.5	0.24	8	3.6	3.2-4.0	0.23
12	13	3.8	3.2-4.5	0.19	13	3.7	3.3-4.0	0.11
13	7	4.0	3.6-4.4	0.21	11	3.9	3.6-4.3	0.16
14	25	3.7	3.2-4.3	0.11	21	3.6	3.0-4.2	0.12
15	24	4.0	3.2-4.7	0.15	24	4.0	3.6-4.6	0.12
16	6	4.0	3.6-4.3	0.22	6	4.0	3.5-4.4	0.24
17	17	3.8	3.4-4.6	0.16	30	3.9	3.4-4.6	0.11
18	8	3.7	3.3-4.2	0.22	15	3.7	3.2-4.5	0.20
19	10	3.6	3.1-4.0	0.19	10	3.6	3.3-4.2	0.16
20	18	3.6	3.1-4.3	0.15	9	3.7	3.0-4.3	0.28
21	13	4.0	3.6-4.4	0.12	9	4.1	3.8-4.5	0.15

TABLE 3.—*Continued.*

11	5	8.3	7.8-9.1	0.42	8	8.2	7.6-9.1	0.37
12	14	7.7	7.0-8.3	0.23	13	7.9	7.2-8.7	0.27
13	7	8.2	7.5-8.8	0.35	11	8.2	7.0-9.3	0.37
14	26	8.2	7.5-8.9	0.15	21	8.0	6.7-9.2	0.28
15	23	8.6	7.7-9.5	0.24	24	8.6	7.7-9.7	0.21
16	6	8.5	7.9-8.9	0.32	6	8.1	7.7-8.9	0.36
17	17	8.3	7.4-9.2	0.28	29	8.4	7.2-9.4	0.18
18	8	8.1	7.4-8.9	0.41	15	7.9	7.0-9.0	0.27
19	10	7.8	6.4-8.5	0.41	10	7.6	6.7-8.2	0.29
20	19	7.8	7.2-8.4	0.16	9	7.8	7.1-8.8	0.43
21	13	8.7	8.1-9.3	0.22	9	8.7	8.1-9.7	0.36
22	5	9.2	8.6-9.9	0.42	17	8.6	7.7-9.4	0.25
23	8	8.7	8.2-9.1	0.24	14	8.7	7.9-9.6	0.26
24	5	7.4	6.9-7.8	0.29	13	7.7	6.9-8.9	0.29
25					2	8.1	7.3-8.9	1.60
26	7	8.9	8.4-9.8	0.37	10	8.7	8.4-9.0	0.18
27	8	8.8	8.2-9.4	0.27	16	8.8	8.2-9.5	0.17
28	26	8.6	7.9-9.4	0.15	33	8.4	7.3-9.3	0.15
29	10	8.7	7.7-9.6	0.41	5	8.4	6.2-9.3	1.14
30	7	8.7	8.3-9.1	0.26	9	8.7	7.8-9.2	0.32
31	3	8.5	7.8-9.2	0.81	3	8.6	8.1-8.9	0.48
32	3	8.4	8.2-8.7	0.29	4	8.3	7.8-8.7	0.42
33	11	8.7	7.4-10.4	0.56	22	8.9	7.9-9.6	0.16
34	6	8.8	8.0-9.7	0.50	17	9.0	7.8-9.8	0.26
35	7	9.1	8.7-10.0	0.36	4	9.2	8.4-9.8	0.58
36	5	9.1	8.4-9.7	0.45	10	8.7	8.1-9.3	0.23
37					1	5.4		
38					2	7.7	7.4-8.0	0.60
39	4	8.5	7.9-9.2	0.61	6	8.8	8.2-9.5	0.43
				Interparietal length				
1	29	4.0	3.3-4.5	0.12	31	3.9	3.3-4.5	0.09
2	10	4.0	3.4-4.3	0.15	7	3.7	3.4-4.1	0.21
3	10	4.2	3.5-4.6	0.19	19	4.0	3.5-4.7	0.13
4	8	4.0	3.6-4.2	0.15	9	3.9	3.6-4.3	0.15
5	10	4.0	3.7-4.3	0.14	14	4.0	3.5-4.4	0.12
6	12	4.0	3.5-4.5	0.16	18	3.8	3.4-4.4	0.13
7	9	3.9	3.5-4.4	0.24	9	4.0	3.6-4.3	0.17
8	15	4.2	3.8-4.6	0.11	7	3.8	3.5-4.0	0.17
9	11	4.0	3.0-4.5	0.25	14	4.1	3.7-4.5	0.12
10	10	3.8	3.2-4.2	0.21	16	3.9	3.3-4.4	0.18
11	5	4.1	3.8-4.5	0.24	8	3.6	3.2-4.0	0.23
12	13	3.8	3.2-4.5	0.19	13	3.7	3.3-4.0	0.11
13	7	4.0	3.6-4.4	0.21	11	3.9	3.6-4.3	0.16
14	25	3.7	3.2-4.3	0.11	21	3.6	3.0-4.2	0.12
15	24	4.0	3.2-4.7	0.15	24	4.0	3.6-4.6	0.12
16	6	4.0	3.6-4.3	0.22	6	4.0	3.5-4.4	0.24
17	17	3.8	3.4-4.6	0.16	30	3.9	3.4-4.6	0.11
18	8	3.7	3.3-4.2	0.22	15	3.7	3.2-4.5	0.20
19	10	3.6	3.1-4.0	0.19	10	3.6	3.3-4.2	0.16
20	18	3.6	3.1-4.3	0.15	9	3.7	3.0-4.3	0.28
21	13	4.0	3.6-4.4	0.12	9	4.1	3.8-4.5	0.15

TABLE 3.—*Continued.*

22	4	3.8	3.5-4.0	0.24	17	3.9	3.3-4.6	0.16
23	8	4.3	3.8-4.6	0.19	14	4.2	3.6-4.5	0.14
24	5	3.7	3.2-4.4	0.43	13	3.9	3.3-4.7	0.22
25					3	4.2	4.1-4.3	0.12
26	7	3.8	3.5-4.4	0.30	10	3.6	3.0-3.8	0.15
27	8	3.8	3.5-4.1	0.14	16	3.8	3.3-4.4	0.15
28	26	3.6	3.0-3.9	0.10	33	3.5	2.5-4.1	0.13
29	10	3.7	3.2-3.9	0.12	6	3.7	3.1-4.1	0.33
30	7	4.0	3.6-4.5	0.22	9	3.8	3.6-4.0	0.10
31	3	3.3	3.1-3.5	0.24	3	3.4	3.3-3.6	0.18
32	3	3.3	3.0-3.7	0.41	4	3.7	3.3-3.9	0.28
33	11	3.9	3.3-4.5	0.23	22	4.0	3.5-4.8	0.14
34	6	4.2	4.0-4.5	0.19	17	4.3	3.6-4.8	0.17
35	7	4.0	3.7-4.7	0.26	4	4.3	4.0-4.5	0.22
36	5	4.1	3.9-4.4	0.17	9	3.9	3.5-4.2	0.16
37					1	3.2		
38					2	3.8	3.6-3.9	0.30
39	4	3.8	3.6-4.0	0.17	6	4.4	3.9-4.9	0.28

External Measurements

Specimens from southern Texas (sample 1) have a total length that averages in the middle of the range for the species (Table 4 and Fig. 9). From southern Texas southward along the Gulf coastal lowlands of Tamaulipas, eastern San Luis Potosí, and northern Veracruz (samples 2-5, 7-10), there is a tendency for specimens to have a progressively shorter total length. Mice from the vicinity of Ebano, San Luis Potosí (8), are the smallest of this series. Specimens from sample 10 (central Veracruz) are somewhat larger than adjacent populations, but are nearly the same size as those from sample 1. The specimens from the Sierra Madre Oriental of Nuevo León and Tamaulipas (6) have a much longer average total length than do those of adjacent coastal areas and more nearly resemble samples from the Mexican Plateau of San Luis Potosí and Zacatecas (samples 33-35). Samples from south of Valle de Mexico in most of Puebla, Morelos, and northern Oaxaca (samples 11-14, 19-20) form a group characterized by medium to short total length. Specimens from central and southern Oaxaca have a long total length; some individuals from these samples are among the longest of the species. Males from the vicinity of Chilpancingo, Guerrero, have a total length that averages intermediate between large mice from the mountains of Oaxaca (16) and the smaller animals from north of the Río Balsas (18). Females from sample 17 and males and females from sample 18 have a total length that is intermediate for the species. Specimens from north of the Río Balsas are somewhat larger than samples from adjacent parts of Morelos (19 and 20), but they do closely resemble specimens in samples from Puebla and northern Oaxaca (11-14). Both males and females from Omilteme, Guerrero (39), have a longer average total length than any other sample of the species. The samples from the Valley of Mexico, Querétaro, Hidalgo, Michoacán, Guanajuato, San Luis Potosí, Aguascalientes, and eastern Jalisco (21-24, 29, 30, 33, 34) form a group characterized by medium to long total length. The shortest males in this group are from sample 23 (245.1) and the shortest females from sample 24 (235.8), whereas the males with the longest average total length are from sample 21 (258.1) and the longest females from sample 34 (254.1). Specimens from central Jalisco (27, 28), along the Río Bolaños in northern Jalisco (32), and extreme southern Zacatecas (31) have a relatively short total length when compared with specimens to the east (29, 30, 33, 34). Females from southern Jalisco (25, 26) have a total length that resembles values from central Jalisco (27, 28), whereas males from sample 26 have a relatively long total length and thereby resemble more closely those in samples to the east. Single females from Soyatlán del Oro (37) and La Laguna (38) in west-central Jalisco have a much longer total length than do specimens in adjacent populations (27, 28). Except for the specimens from Omilteme (39) and Oaxaca (15, 16), the samples from western Zacatecas, Durango, and Chihuahua (35, 36) have the longest mean total lengths for the species.

Variation in length of tail for samples of *Liomys irroratus* followed almost exactly the pattern seen for total length.

Variation in length of hind foot displays a pattern somewhat different from that seen for the other two external measurements. The populations from the lowlands of Texas, Tamaulipas, eastern San Luis Potosí, and northern Veracruz (1-5, 7-10) have hind feet that average nearly the same size. Males from sample 8 and females from samples 4 and 8 have, on the average, the shortest hind feet of this group, whereas males and females from sample 10 have the longest. Males from northern Tamaulipas (2) have hind feet that are somewhat larger than those in adjacent populations, but the females agree perfectly with contiguous samples. Samples from the Valley of Mexico and the central plateau to the north and west (21-24) form a group of samples in which the hind feet average only slightly longer than do those of animals from the lowlands to the east. The hind feet of these mice are shorter than those of specimens to the north on the Mexican Plateau in eastern Jalisco, Zacatecas, San Luis Potosí, Durango, Chihuahua, and in the Sierra Madre Oriental of Tamaulipas and Nuevo León (6, 30, 33-36). Specimens from the northern plateau have hind feet that average among the largest of the species. Those from central Jalisco (27, 28) have shorter hind feet than do populations to the east (30, 33, 34), and mice from around Lago de Chapala (29) have hind feet that are intermediate in size between the small specimens of central Jalisco and the larger specimens to the east in Jalisco, Aguascalientes, and San Luis Potosí. Males in the sample from southern Jalisco (26) have long hind feet, thereby resembling samples from Michoacán, Querétaro, Hidalgo, México, and Distrito Federal, whereas the females from the same sample resemble the smaller-footed mice of central Jalisco. The female from La Laguna, Jalisco (sample 38), has a relatively long hind foot (32.0). Specimens from Puebla, Morelos, and northern Oaxaca (11-14, 19, 20) have short hind feet. Females from southern Morelos (19) have, on the average, the shortest hind feet of the species (average 26.0). Specimens in the two samples from central and southern Oaxaca (15, 16) have hind feet that average among the largest of the species and are noticeably larger than those of mice from northern Oaxaca (13, 14). The hind feet of specimens from Guerrero (17, 18) are somewhat larger than those of the relatively small animals from adjacent parts of Morelos, but resemble closely specimens from western Puebla and northern Oaxaca. Males and females from Omilteme, Guerrero (39), have on the average, for their respective sexes, the largest hind feet of the species.

Cranial Measurements

The 10 cranial measurements analyzed will be discussed below in three groups—1) five measurements dealing with length of the skull (greatest length of skull, length of nasals, length of rostrum, length of maxillary toothrow, and length of interparietal); 2) four measurements dealing with breadth of the skull (zygomatic breadth, interorbital breadth, mastoid breadth, and width of interparietal); 3) one measurement dealing with depth of the skull (depth of braincase).

The samples in the Gulf coastal lowlands of Texas, Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz (1-5, 7-10) form a group characterized by an average greatest length of skull that is of medium length for the species (Tables 3, 4 and Fig. 9); the means range from 31.5 (4) to 32.5 (2) for males and 31.0 (3) and 31.7 (10) for females excepting for those from the vicinity of Ebano, San Luis Potosí, which average considerably smaller than do the other samples (30.6 for males, 30.3 for females). Although specimens from sample 8 are smaller than other members of this group, they are best grouped here. Those from western Puebla, northern Oaxaca, and Morelos (12-14, 19, 20) have, on the average, a short greatest length of skull. Specimens from sample 12 have the shortest mean greatest length of skull for this group (30.7 for males, 30.0 for females). Mean greatest length of skull for specimens from eastern Puebla (vicinity of Tehuacán) is much larger than it is in adjacent populations to the west and south (12-14). The size of these mice is intermediate between the large specimens to the north in Valle de México (21) and the small animals to the south and west (12-14). The large size of these mice may well reflect genetic influence from the adjacent northern populations. Specimens of *L. irroratus* from central and southern Oaxaca (15, 16) have a relatively long mean greatest length of skull that is in the range of those from the northern parts of the Mexican Plateau. In Guerrero, the sample from the vicinity of Chilpancingo (17) and the one from north of the Río Balsas (18) have mean greatest length of skulls that are intermediate in length between those to the southeast (15, 16) and those to the north and east (12-14, 19, 20). Specimens from Omilteme, Guerrero (39), have the longest mean greatest length of skull for the species. Samples from Valle de México, the Mexican Plateau, and adjacent areas (21-25, 29, 30, 33, 36) form a group characterized by a relatively long mean greatest length of skull. Males, and to a less extent females, from western Zacatecas, Durango, and Chihuahua are somewhat larger than other members of this group, but the change is more or less gradual in nature and the difference is not particularly great. Samples from central and northern Jalisco (27, 28, 32) have, on the average, a greatest length of skull that is of medium

TABLE 4.—*Results of three typical SS-STP analyses (total length, greatest length of skull, and zygomatic breadth) of geographic variation in* Liomys irroratus. *Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
		Total length			
39	292.0		39	278.7	
16	270.4		16	268.8	
15	269.3		15	267.1	
35	269.2		35	262.3	
36	266.4		34	254.1	
6	265.9		6	252.7	
26	261.3		36	249.0	
21	258.1		22	248.6	
17	256.5		33	247.3	
33	256.3		23	246.3	
22	255.6		21	242.1	
30	255.1		17	241.7	
34	254.6		29	241.4	
11	250.5		30	241.1	
29	248.3		14	240.1	
2	248.3		18	237.0	
31	247.8		13	236.8	
13	247.3		11	236.4	
24	246.9		31	236.0	
14	245.8		24	235.8	
23	245.1		2	234.2	
1	241.6		10	233.8	
18	240.8		1	231.8	
10	240.7		26	230.7	
3	237.6		25	229.5	
32	235.3		27	227.8	
28	234.6		7	227.5	
12	233.5		3	226.7	
27	233.4		28	226.2	
19	231.0		12	225.8	
9	230.9		32	225.8	
7	230.9		9	223.5	
4	226.3		20	223.1	
5	225.4		5	223.0	
20	223.9		4	217.7	
8	218.7		19	216.6	
			8	211.2	

TABLE 4.—*Continued.*

Greatest length of skull

39	37.0	39	36.1
36	35.5	35	34.6
35	35.5	34	34.3
6	34.8	36	34.1
34	34.2	6	34.1
30	34.1	16	34.1
16	34.1	30	33.4
33	33.8	21	33.3
21	33.8	33	33.3
15	33.7	23	33.3
24	33.5	15	33.3
22	33.4	22	33.0
26	33.4	29	33.0
23	33.3	24	32.9
29	33.1	25	32.9
11	33.0	11	32.5
17	32.8	17	32.2
31	32.6	31	32.2
2	32.5	26	31.8
18	32.2	27	31.8
27	32.1	18	31.7
28	32.1	10	31.7
1	32.0	7	31.5
7	31.9	28	31.4
10	31.8	4	31.3
9	31.8	2	31.3
13	31.7	20	31.3
3	31.7	5	31.3
5	31.5	1	31.3
4	31.5	9	31.1
14	31.4	3	31.0
20	30.9	32	31.0
32	30.9	14	30.8
19	30.8	13	30.6
12	30.7	8	30.3
8	30.6	19	30.2
		12	30.0

TABLE 4.—*Continued.*

Zygomatic breadth

39	17.5	39	17.1
36	17.1	36	16.7
35	16.7	35	16.6
6	16.4	29	16.3
24	16.3	34	16.2
26	16.3	30	16.2
16	16.3	6	16.1
34	16.2	33	16.0
30	16.1	16	16.0
21	16.1	25	16.0
29	16.0	24	16.0
33	16.0	23	15.9
15	15.9	15	15.8
22	15.8	21	15.7
23	15.8	26	15.6
2	15.7	22	15.5
11	15.7	31	15.4
1	15.7	11	15.4
28	15.6	17	15.4
17	15.4	28	15.3
18	15.4	18	15.2
27	15.3	1	15.2
9	15.3	2	15.2
5	15.1	27	15.2
3	15.1	10	15.0
31	15.1	5	14.9
13	15.0	7	14.9
10	15.0	32	14.8
7	14.8	4	14.8
4	14.8	9	14.7
19	14.6	3	14.6
32	14.6	12	14.6
8	14.5	13	14.4
14	14.5	19	14.4
20	14.4	20	14.4
12	14.4	14	14.3
		8	14.3

length—shorter than in samples to the east (29, 30, 33, 34) and three specimens from west-central Jalisco (37, 38). Females from the vicinity of Ciudad Guzmán, Jalisco, have a greatest length of skull that is similar to that of specimens from central Jalisco, whereas males from this area average relatively longer in greatest length of skull, thereby resembling more closely samples from the Mexican Plateau (22-24, 29, 30). Specimens from southern Zacatecas (31) have skulls that average intermediate in length between those of the medium-sized specimens of central Jalisco and the large-sized animals of northern Zacatecas and Aguascalientes.

Variation in length of nasals in *Liomys irroratus* follows closely the pattern of variation for greatest length of skull and the samples appear to fall into about the same groupings. A group of samples along the east coast of México and southern Texas (1-5, 7-10) is characterized by nasals of moderate length. South of the mountains around Mexico City is a series of samples in which the specimens have, on the average, short nasal bones (12-14, 19, 20). Also in central and northern Jalisco (27, 28, 32) are three samples in which specimens have a short mean length of nasals. In central and southern Oaxaca (15, 16) and from Valle de México northward onto the Mexican Plateau and westward on the volcanos of Transverse Volcanic Belt (21-24, 29, 30, 33-36), two groups of samples are characterized by individuals with relatively long nasal bones. Specimens from Omilteme, Guerrero, again have the longest average for the species. Those from the Sierra Madre Oriental of Tamaulipas and Nuevo León have long nasal bones and are best considered with the group from the Mexican Plateau. Specimens from sample 11 are, again, much larger than specimens to the south (14) and west (12, 13) and approach the size of those from the Valley of Mexico (21). Specimens from samples 17 and 18 in Guerrero are intermediate in size between the large specimens to the southeast in Oaxaca and the small mice to the north and east in Morelos and Puebla. Females from southern Jalisco (26) again are best placed with samples from central Jalisco (27, 28), but males are comparatively larger and are intermediate between samples from central Jalisco (27, 28) and those to the east and northeast (22-24, 29, 30). Mean length of nasals for specimens from sample 31 is intermediate between means of samples 27 and 28 (central Jalisco) and those of samples 29, 30, and 33 (eastern Jalisco, Aguascalientes, central Zacatecas, and eastern San Luis Potosí).

Variation in length of rostrum for *Liomys irroratus* is, with only a few exceptions, the same as for the length of nasals. Specimens from sample 8 have an unusually short rostrum, but their geographic position, surrounded as it is by other lowland samples (5, 7, 9) of moderate size, indicates that their affinities must still be with this group. Specimens from samples 11, 17, 18, and 31 are intermediate in size between those of adjacent samples as they were with length of nasal bones. Males from sample 26 (southern Jalisco) have a rostrum that averages no longer than the rostrum of males from the vicinity of Guadalajara (instead of being larger as for greatest length of skull and length of nasals). Both males and females from the vicinity of Lago de Chapala in Jalisco and Michoacán have relatively shorter rostra than they did nasal bones, thereby making them intermediate in size between the medium-sized specimens of central Jalisco (27, 28) and large individuals of extreme eastern Jalisco and San Luis Potosí (30, 33, 34). Males from western Zacatecas, Durango, and Chihuahua have, on the average, rostra that are noticeably longer than those of other samples from the plateau (21-23, 30, 33, 34), but this is not particularly true for females from these areas.

Based on mean length of the maxillary toothrow, samples of *Liomys irroratus* can be divided into two large groups of samples that are not necessarily geographically adjacent. One group is made up of those samples with a mean length of maxillary toothrow of 5.1 or less. Geographically these fall into two subgroups—those from the coastal lowlands of Texas, Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz (1-5, 7-10), and those from Puebla, Morelos, and northern Oaxaca (11-14, 19, 20). It should be noted that specimens from sample 11, which showed tendencies to larger size than other samples from Puebla in greatest length of skull, length of nasals, and length of rostrum, fall within the smaller-sized group in this character. Also, specimens from Guerrero (17, 18), which were intermediate in size for other measurements of cranial length, fit best with these smaller-sized samples based on mean length of the maxillary toothrow. A group of samples, four from Jalisco (26-28, 32), appears to overlap the two major groups of samples in size. The mean length of the maxillary toothrow of this group varies from 5.0-5.2, which is at the upper end of the small-sized samples and the lower end of the large-sized samples. The second major group usually has a mean length of the maxillary toothrow of 5.2 or more. Geographically these samples fall into four groups as follows: 1) central and southern Oaxaca (15, 16); 2) Mexican Plateau south to the Valley of Mexico, westward to eastern Jalisco, and eastward to the Sierra Madre Oriental of Tamaulipas and Nuevo León (6, 21-25, 29-31, 33-36); 3) Omilteme, Guerrero (39); and 4) west-central Jalisco (37, 38). Only two samples—males from sample 23 and females from sample 29—in this group average less than 5.2 and both of these are 5.1. It should be noted that the sample from southern Zacatecas (31), which tended to be somewhat smaller than other Zacatecan samples and those from adjacent areas in other measurements, has a mean length of maxillary toothrow that falls within the group of larger samples. Males from samples 35 and 36 and the females from 36 were larger than might have been expected when compared with mice from contiguous samples.

There is little significant variation in length of the interparietal bone in *Liomys irroratus*. No significant differences were detected among the samples of males with an analysis of variance test and for females only three nonsignificant subsets were present. Essentially, this indicates that the slight differences between samples of the two sexes probably can be best explained as random variation.

Variation in zygomatic breadth of *Liomys irroratus* follows closely the pattern of variation discussed for greatest length of skull, length of nasals, and length of rostrum (Table 4). Specimens from southern Texas and northern Tamaulipas (1, 2) average noticeably broader across the zygomatic arches than do other samples from the lowlands of Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz. The latter group is relatively narrow across the zygomata, with specimens from locality 8 averaging narrowest (males 14.5, females 14.3). Specimens from western Puebla, northern Oaxaca, and Morelos also have a narrow mean zygomatic breadth. However, specimens from central and southern Oaxaca are broad across the zygomatic arches, being much larger than specimens from the northern part of the state, as in most other characters. Specimens from the vicinity of Tehuacán, Puebla, are broad across the zygomatic arches; in fact, they are nearly as large as the sample from the Valley of Mexico (21). Specimens from the vicinity of Chilpancingo, Guerrero (17), and north of the Río Balsas in Guerrero (18) are intermediate in breadth across the zygomatic arches between those from Puebla, Morelos, and northern Oaxaca and those from central and southern Oaxaca as they have been for several other measurements. Another group of samples, which is characterized by relatively broad zygomata, is formed by samples from Valle de México northward on the Mexican Plateau and westward on the Transverse Volcanic Belt, and including the sample from the Sierra Madre Oriental of Tamaulipas and Nuevo León (6, 21-25, 29, 30, 33-36). Mice in samples from western Zacatecas, Durango, and Chihuahua (35, 36) average noticeably larger than do those in other samples of this group and may best be considered in a separate grouping. Both males and females from southern Jalisco (26) have, on the average, a relatively broad zygomatic breadth that resembles the values of samples from the Plateau more closely than those from central Jalisco. The three samples from central and northern Jalisco have narrower mean zygomatic breadths than the samples to the east (29, 30, 33, 34) and the two specimens to the west (37, 38). Specimens from near Moyahua in southern Zacatecas have a narrow mean zygomatic breadth that allies them with mice from samples from central Jalisco (27, 28) rather than larger specimens to the east in Zacatecas, Jalisco, Aguascalientes, and San Luis Potosí (29, 30, 33, 34). Males and females, for their respective sex, from Omilteme, Guerrero, have the broadest average value for zygomatic breadth of the species and are, on the average, 2.1 millimeters broader than males from near Chilpancingo and 1.7 millimeters broader than females.

The pattern of variation present in the interorbital constriction is similar to that seen previously in the length of the maxillary toothrow. For males there is a group of small-sized samples with means of 8.1 or less and a group of large-sized samples with means of 8.2 or more, but for females the dividing point is about 8.0. The small-sized samples are from three geographical areas—the lowlands of Texas, Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz (1-5, 7-10); Puebla, northern Oaxaca, Morelos, and Guerrero (12-14, 17-20); and central and northern Jalisco (27, 28, 32). The males from southern Texas and Tamaulipas (1, 2) average broader across the interorbital region than was expected, but the females from these samples fit with those from the southern samples. Specimens from sample 11 fall at about the dividing point (8.1 for both sexes) between the two major groups, but because they are intermediate between the smaller specimens from contiguous samples to the south (14) and west (12, 13) and larger mice to the north (21), their placement with eigher group would be arbitrary. The large-sized samples are from four geographical areas: central and southern

Oaxaca (15, 16); central México from near Mexico City northward on the Plateau through San Luis Potosí to as far as Chihuahua in the west and the Sierra Madre Oriental of Tamaulipas and Nuevo León in the east, and along the Transverse Volcanic belt into Michoacán and Jalisco (6, 21-26, 29, 30, 33-36); west-central Jalisco (37, 38); Omilteme, Guerrero (39). The specimens from sample 24 have a mean interorbital constriction that is too narrow to be included with the large-sized samples, but mice from all contiguous populations average broad. Specimens from southern Jalisco have, on the average, a broader interorbital region than do those from central and northern Jalisco. Specimens from southern Zacatecas (31) are intermediate in size between animals with a narrower interorbital region from central Jalisco (27, 28) and the broader specimens from the Mexican Plateau (30, 33, 34). Males from samples 35 and 36 and females from sample 35 have a noticeably broader constriction interorbitally than do specimens to the south and east (30, 33, 34).

The pattern of variation displayed in mastoid breadth (Fig. 9) of *Liomys irroratus* is essentially the same as in zygomatic breadth; all the major groupings of samples are the same for the two measurements. In mastoid breadth, however, males from samples 1 and 2 have a mean that is more nearly the same as that for other samples in the lowlands of Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz. Specimens from sample 11 again have a mean value that is intermediate between the small-sized samples in western Puebla and northern Oaxaca (12-14) and the large-sized sample to the north (21). Males from sample 17 have, on the average, a relatively broad mastoid region that is nearly as broad as that of specimens from central and southern Oaxaca, whereas males from sample 18 and females from samples 17 and 18 average narrower across the mastoid region and are intermediate in size between the central and southern Oaxacan (15, 16) samples and those from Morelos, Puebla, and northern Oaxaca (12-14). Males from sample 26 resemble specimens to the east in breadth of the mastoid region, but the females from this sample have a relatively narrow mastoid region, thereby resembling samples from central Jalisco. The three specimens from west-central Jalisco (37, 38) are relatively much narrower across the mastoid region than they were across the zygomatic arches. Values for the three females from samples 37 and 38 fall in the range of the samples from central Jalisco (27, 28). Specimens from southern Zacatecas (32) have a narrow mean mastoid breadth that allies them with the samples from central and northern Jalisco (27, 28, 31) as was the case for zygomatic breadth. Both males and females from samples 35 and 36 are noticeably broader across the mastoid region than mice in samples of the same sex to the south and east on the Mexican Plateau (29, 30, 33, 34). Specimens from sample 39 have the largest mean for the species in mastoid breadth.

Interparietal width exhibits a pattern of variation in *Liomys irroratus* similar to that found in zygomatic breadth and mastoid breadth, but some individual samples display unusual variation that was not predictable based on variation observed in other measurements. Of the medium-sized animals from the lowlands of southern Texas and northeastern México (1-5, 7-10), those from samples 1 and 2 average much narrower in interparietal breadth than do specimens from more southerly samples. Specimens from north-central Veracruz and adjacent Puebla (10) have an interparietal that averages as broad as in the large-sized animals of the Mexican Plateau (21-23, 29, 30, 33, 34). Specimens from sample 11 have a mean interparietal breadth that falls with other samples from Puebla, northern Oaxaca, and Morelos (12-14, 19, 20). Males from central (15) and southern (16) Oaxaca and females from central Oaxaca average slightly larger than do samples to the north, but females from southern Oaxaca average slightly smaller than do those from sample 13. The placement of the Guerreran samples (17, 18) is difficult because the differences between contiguous samples are relatively small. Specimens from Omilteme, Guerrero (39), have a mean interparietal width that is not much broader than in specimens from the vicinity of Chilpancingo. Most of the large-sized animals from Mexico City northward have relatively broad interparietal bones (6, 21-23, 29, 30, 33-36). One exception to this is the specimens from north-central Michoacán (24) which have unusually narrow interparietal bones (7.4 for males, 7.7 for females). The medium-sized animals from central and northern Jalisco have a mean interparietal width that is as broad as in the larger specimens to the east (29, 30). Specimens from southern Zacatecas (31) have interparietal bones that average narrower than the interparietals of specimens from surrounding samples. The three large-sized specimens from west-central Jalisco (37, 38) have interparietal bones that are much narrower than the interparietals of the smaller specimens of central Jalisco (27, 28).

The pattern of variation in depth of the braincase (Fig. 9) in *Liomys irroratus* is similar to the pattern seen in several other measurements (for example mastoid breadth). Specimens from the lowlands of Texas, Tamaulipas, Nuevo León, San Luis Potosí, and Veracruz (1-5, 7-10) form a group characterized by a relatively shallow braincase. Samples from south of the mountains around Mexico City in Puebla, Morelos, and northern Oaxaca form another group in which the braincase is, on the average, relatively shallow. Specimens from Guerrero (17, 18) have an average depth of braincase that is nearer that of specimens from Puebla, Morelos, and northern Oaxaca than specimens from central and southern Oaxaca (15, 16), which have relatively deep braincases. Specimens from Omilteme, Guerrero, have, on the average, the deepest braincases of the species. The samples from Mexico City northward on the Mexican Plateau to Chihuahua in the west and into the Sierra Madre Oriental (6, 21-25, 30, 33-36) of Nuevo León in the east form a group characterized by deep braincases. Of this group those from samples 35 and 36 have the largest mean values. Specimens from central and northern Jalisco (27, 28, 32) have on the average shallower braincases than do specimens to the east (21-25, 30, 33, 34). Males from southern Jalisco (26) are intermediate in size between the males from central Jalisco and those to the east, whereas females from this sample have shallow braincases as do females from central Jalisco. Specimens from the vicinity of Lago de Chapala in Jalisco and Michoacán (29) have a mean depth of braincase that is the same as for specimens from sample 27 in central Jalisco. Specimens from southern Zacatecas (31) are intermediate in size between those from central Jalisco and those from the

Mexican Plateau. The two specimens (37, 38) from west-central Jalisco have deep braincases.

Qualitative Cranial Characters

Condition of interparietal bone (Table 5).—Only nine (1, 2, 4, 8, 13, 18, 19, 25, 38) of the 39 samples of *Liomys irroratus* were found to have no individuals with the interparietal bone divided in half. Samples from southern Texas and coastal northeastern México (1-5, 8, 9), excepting those from Veracruz (7, 10), have a relatively low percentage of individuals with the interparietal bone divided. This is also true of samples from Puebla, Morelos, and northern Oaxaca (11-14, 19, 20). It should be noted that sample 11 has a low percentage of individuals with the interparietal bone divided as in other samples from Puebla and unlike the samples to the north. None of the 32 individuals examined from sample 18 had the bone divided, but six of 45 individuals from the vicinity of Chilpancingo (17) were found to have divided interparietals. A somewhat higher percentage of individuals from central and southern Oaxaca (15, 16) had the interparietal divided than in samples to the north in Oaxaca and Puebla (11-14). More than 20 per cent of the individuals from samples from north and west of Mexico City (6, 21-23, 26-31, 33-35, 37) excepting 24, 25, 32, 36, and 38 have a divided interparietal; in two samples from there in which less than 20 per cent of the individuals had the interparietal divided, the percentage with this condition was 12.5 (32) and 18.7 (36).

Samples of *Liomys irroratus* from the northeastern part of the range of the species (1-10) have a high percentage of the individuals with the posterior margin of the interparietal unnotched. In all of these samples (including the specimens, sample 6, from the Sierra Madre Occidental of Nuevo León and Tamaulipas), with the exception of the sample from northern Veracruz (7), more than 50 per cent of the individuals have an unnotched interparietal. A high percentage of individuals (more than 50 per cent) with the posterior margin of the interparietal unnotched also is characteristic of samples from Puebla and northwestern Oaxaca (11-13), Guerrero south of the Río Balsas (17), vicinity of Mexico City northward in México, Hidalgo, and Querétaro (21, 22), and central and western San Luis Potosí, Aguascalientes, northeastern Jalisco, and eastern Zacatecas (33, 34). The remainder of the samples contain 40 per cent or less of individuals with the posterior margin of the interparietal unnotched. The areas in which this characteristic occurs in the lowest frequency are northeastern and central Oaxaca (14, 15) and Omilteme, Guerrero (39).

Condition of posterior nasal region (Table 6).—Samples from San Luis Potosí northward to Chihuahua and Texas and southward through northeastern Jalisco, Querétaro, Hidalgo, México, and Distrito Federal (1-6, 8, 9, 21-23, 29-36) are characterized by approximately one half or more of the specimens having the posterior margin of the nasal bone truncated. The two samples from Veracruz (7, 10) have a relatively low percentage of individuals with the nasals truncated posteriorly. Samples (12-20, 39) from south of Mexico City in Puebla, Morelos, Guerrero, and Oaxaca (excepting sample 11) also have a low percentage of in-

TABLE 5.—*Geographic variation in the configuration of the interparietal bone of* Liomys irroratus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Interparietal bone			Posterior margin of interparietal bone			
Sample	N	Undivided	Divided	N	Notched	Slightly notched	Unnotched
1	69	100.0	0	68	1.5	11.8	86.7
2	24	100.0	0	24	8.3	8.3	83.4
3	41	95.1	4.9	40	20.0	17.5	62.5
4	30	100.0	0	31	16.1	25.8	58.1
5	63	93.7	6.3	63	17.5	31.7	50.8
6	42	64.3	35.7	40	7.5	40.0	52.5
7	24	62.5	37.5	23	30.4	34.8	34.8
8	32	100.0	0	32	15.6	15.6	68.8
9	47	91.5	8.5	47	23.1	14.9	63.8
10	46	73.9	26.1	46	26.1	21.7	52.2
11	17	94.1	5.9	15	40.0	0	60.0
12	35	97.1	2.9	35	5.7	22.9	71.4
13	22	100.0	0	57	8.8	35.1	56.1
14	81	93.8	6.2	42	54.8	28.6	16.6
15	54	81.5	18.5	54	57.4	29.6	13.0
16	13	76.9	23.1	12	41.7	25.0	33.3
17	45	86.7	13.3	46	10.9	6.5	82.6
18	32	100.0	0	32	34.4	25.0	40.6
19	16	100.0	0	16	37.5	25.0	37.5
20	32	96.9	3.1	32	18.8	43.7	37.5
21	30	76.7	23.3	30	13.3	30.0	56.7
22	31	54.8	45.2	31	19.4	25.8	54.8
23	33	84.8	15.2	29	31.0	27.6	41.4
24	34	94.1	5.9	38	63.2	18.4	18.4
25	4	100.0	0	4	50.0	0	50.0
26	32	46.9	53.1	32	43.8	15.6	40.6
27	34	67.6	32.4	33	54.5	18.2	27.3
28	50	68.0	32.0	50	34.0	24.0	42.0
29	32	62.5	37.5	32	46.9	28.1	25.0
30	21	52.4	47.6	21	42.9	38.1	19.0
31	4	75.0	25.0	4	50.0	25.0	25.0
32	16	87.5	12.5	17	41.2	29.4	29.4
33	40	50.0	50.0	38	31.6	7.9	60.5
34	43	69.8	30.2	44	25.0	27.3	47.7
35	9	66.7	33.3	9	55.6	11.1	33.3
36	16	81.3	18.7	16	56.3	18.7	25.0
37	5	40.0	60.0	5	20.0	40.0	40.0
38	2	100.0	0	2	0	0	100.0
39	15	93.3	6.7	14	78.6	14.3	7.1

TABLE 6.—*Geographic variation in bones of the posterior portion of the nasal-premaxillary complex of* Liomys irroratus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Shape of posterior margin of nasals				Length of premaxillary bones		
Sample	N	Emarginate	Rounded	Truncate	N	Longer than nasals	Equal to nasals
1	72	1.4	5.5	93.1	72	100.0	0
2	24	4.2	12.5	83.3	24	87.5	12.5
3	40	20.0	22.5	57.5	40	100.0	0
4	35	20.0	25.7	54.3	31	100.0	0
5	61	26.2	24.6	49.2	66	98.5	1.5
6	42	9.5	31.0	59.5	42	100.0	0
7	26	30.8	53.8	15.4	25	100.0	0
8	33	12.1	6.1	81.8	31	100.0	0
9	51	17.6	9.8	72.6	50	98.0	2.0
10	28	28.6	46.4	25.0	49	100.0	0
11	37	8.1	51.4	40.5	16	100.0	0
12	34	26.5	47.0	26.5	34	100.0	0
13	22	45.4	27.3	27.3	23	100.0	0
14	87	32.2	42.5	25.3	82	98.8	1.2
15	49	75.5	22.4	2.1	55	92.7	7.3
16	13	61.5	38.5	0	13	100.0	0
17	48	47.9	22.9	29.2	48	100.0	0
18	33	30.3	48.5	21.2	32	100.0	0
19	16	68.8	18.7	12.5	16	100.0	0
20	34	38.2	47.1	14.7	35	100.0	0
21	34	14.7	5.9	79.4	33	100.0	0
22	35	11.4	20.0	68.6	35	100.0	0
23	33	12.1	27.3	60.6	33	100.0	0
24	35	57.1	34.3	8.6	34	100.0	0
25	5	20.0	20.0	60.0	5	100.0	0
26	23	18.2	48.5	33.3	33	100.0	0
27	34	2.9	50.0	47.1	34	100.0	0
28	50	10.0	32.0	58.0	50	100.0	0
29	33	3.0	12.1	84.9	32	100.0	0
30	22	31.8	18.2	50.0	23	100.0	0
31	4	25.0	25.0	50.0	4	100.0	0
32	16	12.5	31.3	56.2	16	100.0	0
33	40	20.0	30.0	50.0	41	100.0	0
34	45	15.6	13.3	71.1	45	100.0	0
35	9	44.4	11.2	44.4	9	100.0	0
36	15	6.7	13.3	80.0	15	100.0	0
37	5	20.0	60.0	20.0	5	100.0	0
38	2	0	100.0	0	2	100.0	0
39	15	20.0	80.0	0	15	100.0	0

dividuals with truncated nasals. Lowest values for the species for truncate nasals are those from central and southern Oaxaca (15, 16) and Omilteme, Guerrero (39). To the north of Mexico City a relatively small percentage of individuals with the posterior margin of the nasals truncated was recorded for samples from north-central Michoacán (24), southern Jalisco (26), and western Jalisco (37, 38, the latter based on only two specimens). The value for sample 11 is intermediate between that for other samples from Puebla and those for samples to the northwest around Mexico City.

In only 10 individuals from five localities throughout the range of *Liomys irroratus* were the nasal and premaxillary bones found to terminate at the same level; in all others, the nasal bones terminated anterior to the premaxillary bones. The most individuals from one sample with nasals terminating at the same point as premaxillaries was four from central Oaxaca (15); the highest percentage of individuals from one locality having this condition was 12.5 per cent—from extreme northern Tamaulipas (2).

Multivariate Analysis

The 13 external and cranial measurements and three qualitative cranial characters (the position of the posterior termination of the nasal and premaxillary bones was not used because of the small amount of variation present) were analyzed using the NT-SYS multivariate programs. Phenograms diagramming the phenetic relationships of both males and females of *Liomys irroratus* were computed from both distance and correlation matrices; the phenograms based upon the distance matrices are presented herein because they have the larger coefficients of cophenetic correlation (Fig. 10). In addition, a map (Fig. 11) including values for both sexes is presented showing the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components were computed from the matrix of correlation among the 16 characters; these first three components combine to express 83.93 per cent of the phenetic variation in males and 79.83 per cent in females. Two-dimensional plots of principal components I-II and I-III and a three-dimensional projection of the 39 samples onto the first three principal components based on the matrix of correlation among characters are presented for both sexes (Figs. 12-15).

The distance phenogram for male *Liomys irroratus* shows the samples falling into three major groups. The group at the top of the phenogram represents small- to medium-sized rats and includes material from three geographic areas: 1) southern Texas and northeastern México as far south as central Veracruz (1-5, 7-10); 2) Puebla, Morelos, northern Oaxaca, and Guerrero (12-14, 17-20); and 3) northern Jalisco (32). The samples tend to fall into groupings with those from northeastern México toward the top of the cluster and those from south of the Transverse Volcanic Belt toward the bottom. However, the sample from the vicinity of Ebano, San Luis Potosí (8), does fall near the bottom of the cluster. As was noted in the univariate analysis, individuals from this area were generally much smaller than those from surrounding areas. Within this cluster of samples,

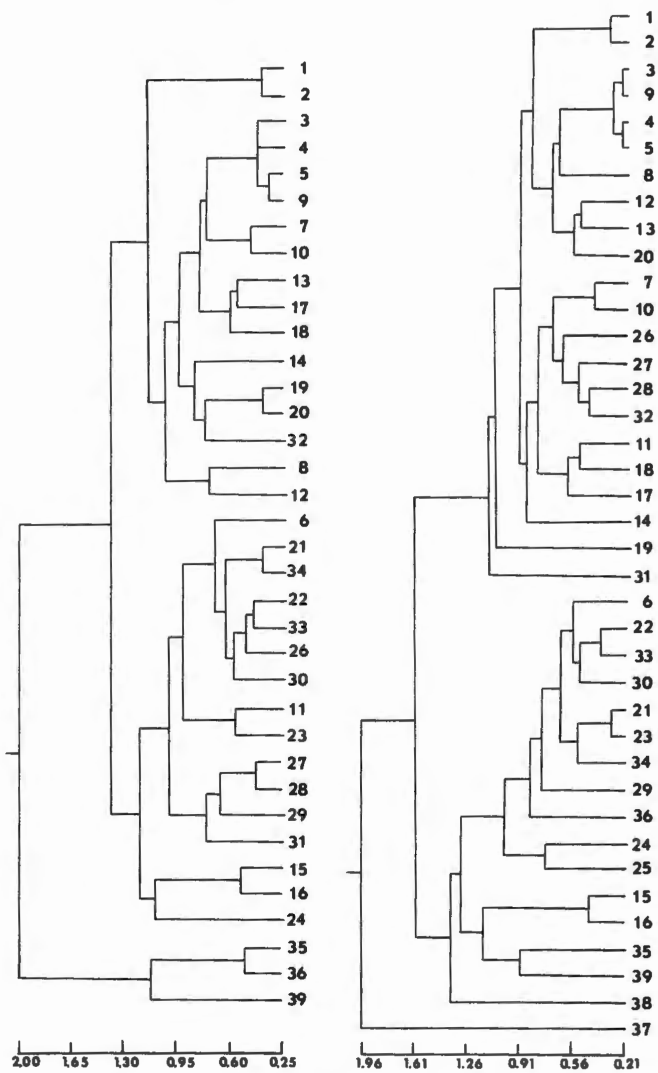


FIG. 10.—Phenograms of numbered samples (see Fig. 8 and text) of *Liomys irroratus* (males left, females right) computed from distance matrices based on standaridized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram for males is 0.722 and for females is 0.728.

the two from southern Texas (1) and extreme northern Tamaulipas (2) are phenetically the most distant from the other samples.

The middle cluster of samples is geographically from 1) the vicinity of Mexico City northward on the Mexican Plateau, into the Sierra Madre Oriental of Nuevo León in the northeast, and as far west as central Jalisco and Zacatecas (6, 21-24, 26-31, 33, 34); 2) central and southern Oaxaca (15, 16); and 3) vicinity of Tehuacán, Puebla (11). Within the major cluster are three subclusters of sam-

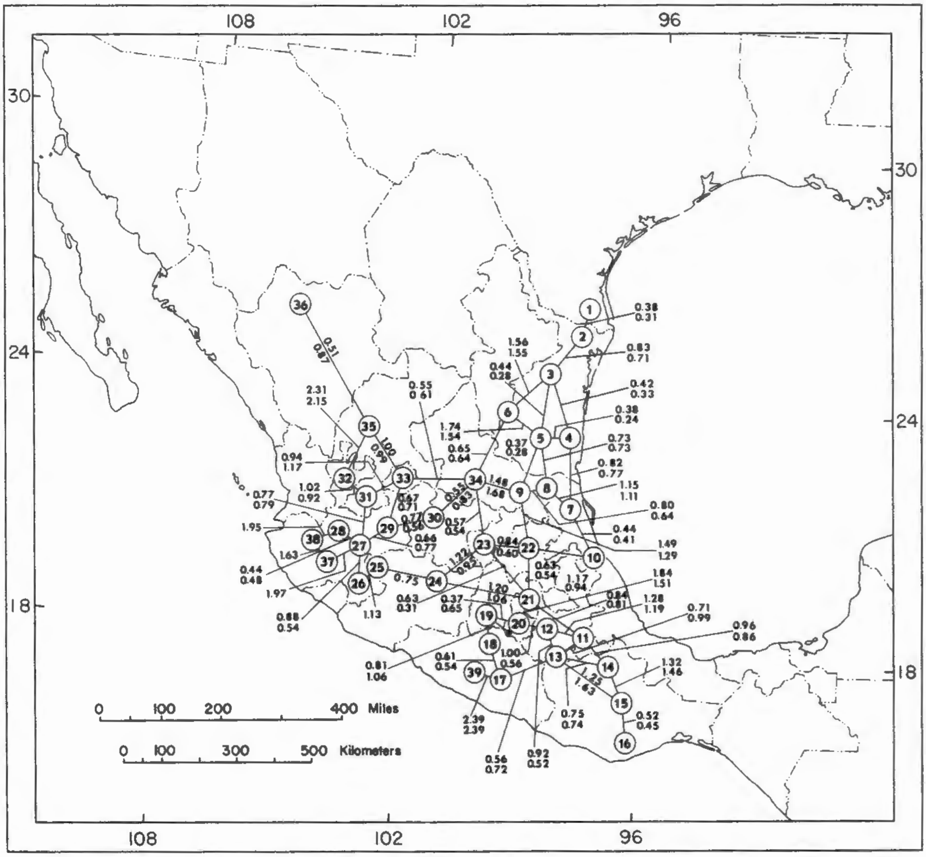
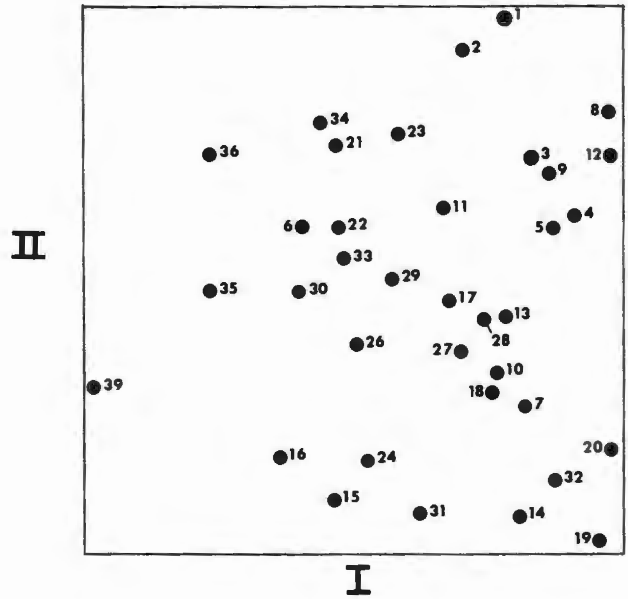


FIG. 11.—Map showing selected distance coefficients (from distance matrices) between samples of *Liomys irroratus* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 8 and text for key to samples.

ples, which segregate relatively well along geographical lines. One subcluster consists of samples from the Valley of Mexico northward into San Luis Potosí, Tamaulipas, and Nuevo León in the northeast and into eastern and southern Jalisco, Aguascalientes, and Zacatecas in the northwest (6, 21-23, 26, 30, 33, 34). It is of interest to note that the males from southern Jalisco (26) cluster with samples from the Mexican Plateau, whereas in the analysis for females, as will be seen later, they cluster with samples from central Jalisco (27, 28). Also included in this group is the sample from the vicinity of Tehuacán, Puebla, which falls with other samples from Puebla and northern Oaxaca in the analysis of females. The second subcluster includes samples from central Jalisco and southern Zacatecas (27-29, 31). In the analysis of females, the easternmost of the Jaliscan samples (29) groups with the samples from the Mexican Plateau. The last of the subclusters in this middle group consists of samples from two geographical areas—central and southern Oaxaca (15, 16), and north-central Michoacán (24).

TABLE 7.—*Factor matrix from correlation among 16 characters of* Liomys irroratus *studied.*

Character	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Total length	−0.931	−0.075	0.190	−0.916	0.118	−0.163
Length of tail	−0.757	−0.180	0.268	−0.746	0.162	−0.323
Length of hind foot	−0.936	−0.051	0.058	−0.882	0.263	0.182
Greatest length of skull	−0.985	0.076	0.048	−0.988	−0.029	0.046
Zygomatic breadth	−0.944	0.175	0.051	−0.935	−0.181	0.108
Interorbital constriction	−0.917	0.248	−0.029	−0.877	−0.078	0.230
Mastoid breadth	−0.937	0.114	0.040	−0.976	−0.031	0.077
Length of nasals	−0.915	0.233	0.091	−0.918	−0.245	0.087
Length of rostrum	−0.953	−0.066	0.169	−0.972	−0.071	−0.072
Length of maxillary toothrow	−0.860	−0.023	−0.050	−0.882	−0.296	−0.138
Depth of braincase	−0.963	−0.035	−0.015	−0.880	−0.276	0.024
Interparietal width	−0.628	−0.051	−0.583	−0.361	0.741	0.174
Interparietal length	−0.071	0.711	0.354	−0.426	0.619	0.469
Posterior margin of interparietal	0.512	0.671	0.078	0.404	−0.381	0.512
Division of interparietal	−0.486	−0.131	−0.750	−0.385	−0.208	−0.183
Posterior margin of nasals	0.037	0.768	−0.504	0.107	−0.263	0.819



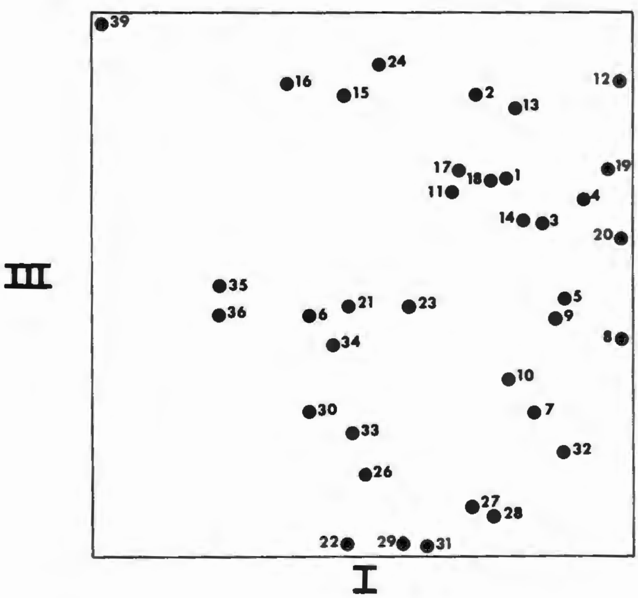


FIG. 12.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 36 samples of male *Liomys irroratus*. Top, component I plotted against compoeent II; bottom, component I plotted against component III. See Fig. 8 and text for key to samples.

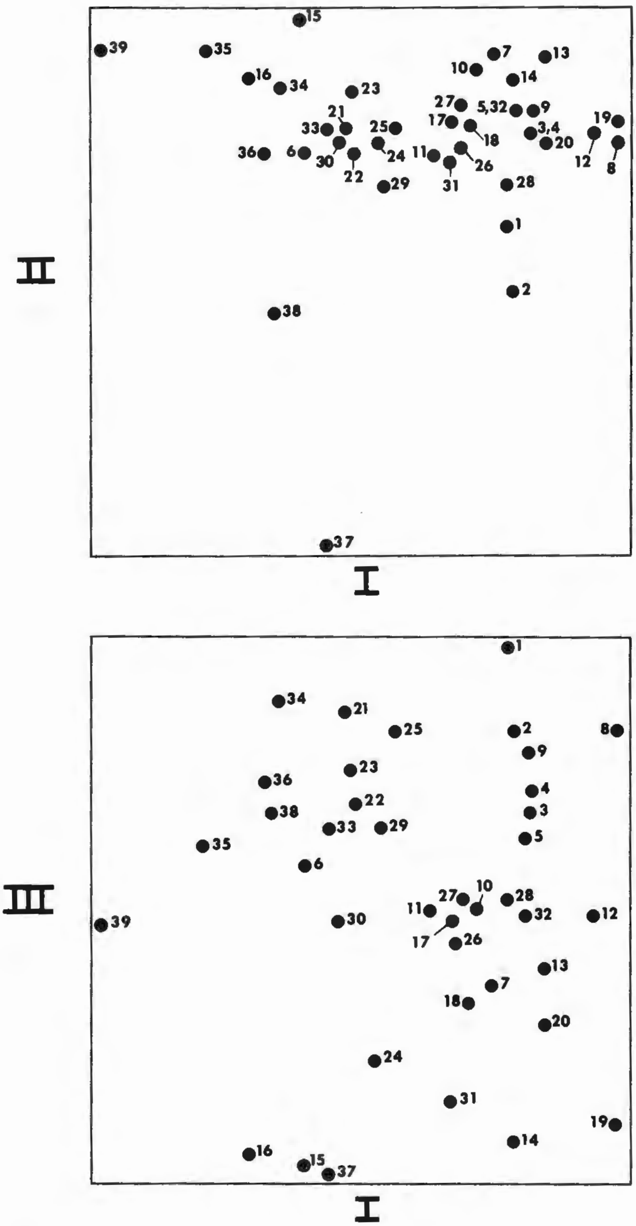


FIG. 13.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 39 samples of female *Liomys irroratus*. Top, component I plotted against component II; bottom, component I plotted against component III. See Fig. 8 and text for key to samples.

The third major cluster of samples of males, at the bottom of the distance phenogram, contains the largest individuals of the species. The samples are from two geographical areas; one is Omilteme, Guerrero (39), and the other is northern Jalisco, western Zacatecas, Durango, and Chihuahua (35, 36).

The distance phenogram based on values for female *Liomys irroratus* also clusters the samples into three major groups, but the composition of these groups is somewhat different than those of males. The upper cluster in this phenogram contains samples from southern Texas, northeastern México, Veracruz, Puebla, Morelos, Guerrero, northern Oaxaca, and northern Jalisco (1-5, 7-14, 17-20, 32) as it did for males, but includes also the samples from central and southern Jalisco (26-28) and southern Zacatecas (31) that were grouped with the Mexican Plateau samples for males. It should be noted also that sample 11, which was grouped with the Mexican Plateau samples based on values for males, is placed with the other Pueblan samples based on female values. The second major cluster of samples includes those from the Mexican Plateau north of Mexico City into Nuevo León and Chihuahua (21-25, 29, 30, 33-36), from central and southern Oaxaca (15, 16), Omilteme, Guerrero (39), west-central Jalisco (38). The sample from the vicinity of Lago de Chapala (29) was placed with those from central Jalisco based on values for males and those from Omilteme (39) and northern Jalisco, western Zacatecas, Durango, and Chihuahua (35, 36) were placed in a separate group based on the data for males. The small sample from the Sierra del Tigre in Jalisco (25), which is represented only by female specimens, was placed in this group. The third major group is based upon a single specimen from Soyatlán del Oro, Jalisco (37), that has an unusually small interparietal bone, which probably accounts for its rather "distant" separation from the second cluster of samples.

The amount of phenetic variation represented in the first three principal components for males and females, respectively, of *Liomys irroratus* was 63.79 and 60.73 for component I, 11.11 and 9.80 for component II, and 9.04 and 9.29 for component III. Results of a factor analysis showing characters influencing the first three components is given in Table 7. From the factor analysis, it can be seen that the first, and by far the most important, component is heavily influenced by general size; components II and III are influenced by size of the interparietal bone and the qualitative cranial characters. Examination of the two-dimensional plots (Figs. 12, 13) and the three-dimensional plots (Figs. 14, 15) of the samples reveal a pattern similar to that of the distance phenogram, but in some ways differing from it. The samples on the right-hand side of the three-dimensional projection for males represents the same group that was found in the upper part of the distance phenogram (1-5, 7-14, 17-20, 32) but grouped with these are the samples from central Jalisco (27, 28) and the sample from the vicinity of Tehuacán, Puebla (11), which were included in the middle cluster of the distance phenogram. The position of sample 11 is nearly intermediate between samples 13 and 14, to the south and west and sample 21 to the northwest. This pattern was evident in several of the measurements in the univariate analysis. Samples 23, 29, and 31 lie between the two clusters of samples, although they were included with the central cluster in the distance phenogram. The positions of samples 29 and

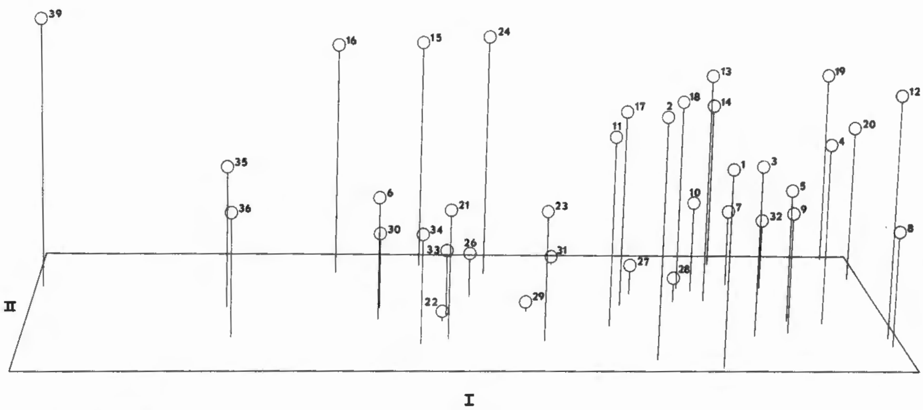


FIG. 14.—Three-dimensional projection of 36 samples of male *Liomys irroratus* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and three qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 8 and text for key to samples.

31 are intermediate between populations that are contiguous with them (27 and 30 for 29, and 27 and 33 for 31). The central group of samples are from two geographic areas—Mexican Plateau north of Mexico City into Nuevo León in the northeast and central Zacatecas in the northwest (6, 21-24, 26, 30, 33, 34), and central and southern Oaxaca (15, 16). Still included with this group is the sample from southern Jalisco (26). The two samples (35, 36) from extreme northern Jalisco, western Zacatecas, Durango, and Chihuahua form a group by themselves as does the sample from Omilteme, Guerrero (39).

The three-dimensional projection for females has on the right-hand side those samples that cluster in the upper part of the distance phenogram. These samples are from three geographic areas as follows: 1) southern Texas and northeastern México as far south as central Veracruz (1-5, 7-10); 2) Puebla, Morelos, northern Oaxaca, and Guerrero (11-14, 17-20); and 3) southern, central, and northern Jalisco and southern Zacatecas (26-28, 31, 32). Sample 11, although it does fall within this group, is situated phenetically about halfway between samples from western Puebla and northern Oaxaca (13, 14) and the sample from Valle de México. The samples in the center of the plot also are from three geographic areas as follows: 1) Mexican Plateau north to Nuevo León in the northeast and Chihuahua in the northwest (6, 21-25, 29, 30, 33-36); 2) central and southern Oaxaca (15, 16); and 3) La Laguna, Jalisco (38). The sample from extreme northern Jalisco and western Zacatecas (35) is somewhat removed from the remainder of the group. Samples 25 and 29 are located at the far right of this central group, which is of interest because they are contiguous with populations in central and southern Jalisco that are included in the group of samples at the right. The single specimen from Soyatlán del Oro, Jalisco (37), is separated from the other localities being located at the backside of the projection probably as the result of its small interparietal bone, which is a character that is heavily weighted

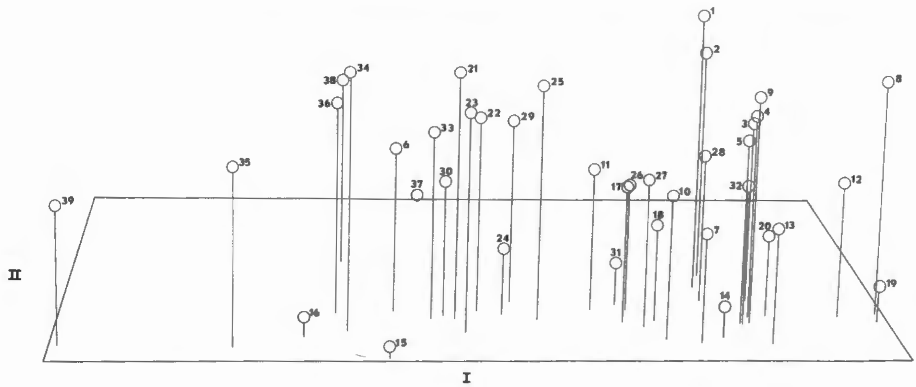


FIG. 15.—Three-dimensional projection of 39 samples of female *Liomys irroratus* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and three qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 8 and text for key to samples.

in this component. The sample from Omilteme, Guerrero (39), located at the far left of the plot, is phenetically quite distant from other samples of *Liomys irroratus.*

Variation in Color

The range of color variation in *Liomys irroratus* (Fig. 16 and Table 8), as with other species of *Liomys,* is not extensive; the means for red reflectance ranged from 10.6 to 16.8, those for green reflectance from 5.8 to 9.3, and those for blue reflectance from 5.5 to 9.0 in the 46 samples studied for color (samples differ from those used in the univariate analysis because color values were not available for all univariate samples and color exhibits much more microgeographic variation than do external and cranial measurements). As will be seen in other species, mice from low, arid situations are palest in color (highest reflectance), whereas those from high, moist areas are darkest. The palest samples of *irroratus* examined were from southern Puebla (20) and coastal Tamaulipas (4, 9), whereas the darkest examined were from Omilteme, Guerrero (24), Cerro San Felipe, Oaxaca (16), Miquihauna, Tamaulipas (8), and Metlaltoyuca, Puebla (13). The samples from the Gulf coastal lowlands of northeastern México and southern Texas generally have high readings, but samples from Veracruz, which grouped with them on mensural data, have relatively low color reflectance readings. Also, the sample from the vicinity of Monterrey and Linnares in Nuevo León has a much lower average color reading than do samples from coastal areas of Tamaulipas. The range of values for red reflectance for samples from the vicinity of Mexico City northward on the Mexican Plateau is from 11.9 (in Querétaro) to 15.2 (in Zacatecas), indicating relatively little color variation in this area. Hooper (1947: 47) in describing *L. i. pullus* from the Valley of Mexico stated that it was much darker than mice from adjacent samples of *L. i. alleni* and more closely resembled

TABLE 8.—*Geographic variation in dorsal coloration of 46 samples of* Liomys irroratus. *Samples differ from those used for univariate and multivariate analyses (see text).*

		Red			Green			Blue		
Sample	N	Mean ± 2 SE	Range	CV	Mean ± 2 SE	Range	CV	Mean ± 2 SE	Range	CV
1 (Texas:Brownsville)	10	15.3 ± 0.94	(13.5-19.0)	9.8	7.8 ± 0.45	(7.0-8.5)	9.1	7.2 ± 0.37	(6.5-8.5)	8.0
2 (Tamaulipas:San Fernando)	7	15.7 ± 0.81	(14.5-17.5)	6.8	9.0 ± 0.28	(8.5-9.5)	5.6	8.4 ± 0.47	(7.5-9.5)	7.5
3 (Nuevo León:Linnares, Monterrey)	6	12.8 ± 0.56	(12.0-14.0)	5.4	7.7 ± 0.61	(7.0-9.0)	9.8	7.0 ± 0.26	(6.5-7.5)	4.6
4 (Tamaulipas:Soto la Marina)	10	16.0 ± 0.54	(14.5-17.5)	5.4	8.5 ± 0.30	(7.5-9.0)	5.5	8.0 ± 0.23	(7.5-8.5)	4.7
5 (Tamaulipas:Victoria)	10	14.1 ± 0.88	(11.5-16.0)	9.9	8.1 ± 0.48	(7.0-9.5)	9.4	7.6 ± 0.48	(6.0-9.0)	10.1
6 (Tamaulipas:Piedra)	10	14.3 ± 0.86	(12.5-17.0)	9.5	8.1 ± 0.31	(7.5-9.0)	6.2	7.3 ± 0.22	(7.0-8.0)	4.8
7 (Nuevo León:Iturbide, Zaragoza)	8	12.9 ± 0.72	(12.5-15.0)	8.0	8.1 ± 0.58	(7.5-9.5)	10.2	7.4 ± 0.51	(6.5-8.5)	9.7
8 (Tamaulipas: Miquihauna)	3	11.5 ± 0.58	(11.0-12.0)	4.3	6.5 ± 1.00	(6.0-7.5)	13.4	6.3 ± 0.23	(6.0-6.5)	4.6
9 (Tamaulipas:Altamira, Tampico)	5	16.0 ± 0.71	(15.0-17.0)	4.9	9.0 ± 0.45	(8.5-9.5)	5.6	8.4 ± 0.27	(8.0-9.0)	5.0
10 (San Luis Potosí: Valles)	15	15.1 ± 0.53	(13.5-16.5)	6.8	7.6 ± 0.30	(7.0-8.5)	5.4	7.5 ± 0.21	(7.0-8.0)	7.6
11 (Veracruz:Tuxpan)	10	11.9 ± 0.57	(11.0-14.0)	7.6	7.2 ± 0.49	(6.5-9.0)	10.9	6.8 ± 0.48	(6.0-8.5)	11.1
12 (Veracruz: Tlapacoyon)	5	11.7 ± 1.29	(10.0-14.0)	12.3	6.7 ± 0.40	(6.5-7.5)	6.7	6.4 ± 0.58	(6.0-7.5)	10.2
13 (Puebla: Metlaltoyuca)	5	11.5 ± 0.95	(10.5-13.0)	9.2	6.1 ± 0.58	(5.5-7.0)	10.7	5.5 ± 0.55	(5.0-6.5)	11.1

TABLE 8.—*Continued.*

14 (Oaxaca:Cuicatlán)	15	12.6 ± 0.71	(10.5-15.5)	10.9	7.3 ± 0.46	(6.5-9.5)	12.3	6.7 ± 0.38	(5.5-8.5)	11.1
15 (Oaxaca:Oaxaca)	15	13.3 ± 0.42	(11.5-14.5)	6.2	6.9 ± 0.31	(5.5-8.0)	8.9	6.8 ± 0.36	(5.5-8.0)	10.3
16 (Oaxaca:Cerro San Felipe)	2	10.8 ± 0.50	(10.5-11.0)	3.3	5.8 ± 0.50	(5.5-6.0)	6.1	5.5	(5.5)	
17 (Oaxaca:Mt. Zempoaltepec)	4	11.6 ± 1.93	(9.0-13.5)	16.6	6.6 ± 1.38	(5.0-8.0)	20.8	5.9 ± 1.31	(4.0-7.0)	22.3
18 (Oaxaca:San Pedro Jilotepec)	1	12.0			8.0			7.0		
19 (Puebla:Izúcar de Matamoros)	10	14.4 ± 0.45	(13.5-16.0)	4.9	8.4 ± 0.44	(7.5-10.0)	8.3	8.1 ± 0.35	(7.5-9.0)	6.8
20 (Puebla:Acatlán, Tehuitzingo)	6	16.8 ± 1.56	(15.0-19.5)	11.5	9.0 ± 0.77	(8.0-10.0)	10.6	8.4 ± 0.75	(7.5-9.5)	10.9
21 (Morelos:Puente de Ixtla)	4	12.5 ± 0.71	(11.5-13.0)	5.7	6.8 ± 0.29	(6.5-7.0)	4.3	6.8 ± 0.29	(6.5-7.0)	4.3
22 (Guerrero:Teololoapan, Texcalzintla)	10	13.6 ± 0.77	(12.5-16.5)	9.0	7.8 ± 0.48	(7.0-9.5)	9.6	7.3 ± 0.37	(6.5-8.5)	8.1
23 (Guerrero:Agua del Obispo)	10	12.8 ± 0.83	(10.5-15.0)	10.4	7.8 ± 0.48	(6.5-9.0)	9.7	7.3 ± 0.45	(6.5-8.5)	9.7
24 (Guerrero:Omilteme)	7	10.6 ± 0.75	(9.5-12.0)	9.3	6.6 ± 0.34	(6.0-7.0)	6.8	6.3 ± 0.43	(5.5-7.0)	9.1
25 (Distrito Federal and adjacent parts of México)	8	13.1 ± 0.88	(11.5-15.0)	9.5	7.9 ± 0.77	(6.5-9.5)	13.8	7.4 ± 0.55	(6.5-8.5)	10.4
26 (Hidalgo:Actopan, Ixmiquilpan)	2	13.5 ± 2.00	(12.5-14.5)	10.4	7.5			7.3 ± 0.50	(7.0-7.5)	4.8
27 (Querétaro:Jalpan)	8	11.9 ± 0.81	(10.0-13.5)	9.6	6.4 ± 0.40	(6.0-7.5)	8.7	5.9 ± 0.40	(5.5-6.5)	9.4
28 (Querétaro:Pinal de Amoles)	5	11.9 ± 0.73	(11.0-13.0)	6.9	6.2 ± 0.68	(5.5-7.0)	12.3	6.0 ± 0.32	(5.5-6.5)	5.8
29 (Querétaro:Querétaro)	5	13.7 ± 1.17	(12.5-15.5)	9.5	8.1 ± 0.37	(7.5-8.5)	5.2	7.9 ± 0.49	(7.5-8.5)	7.0

TABLE 8.—*Continued.*

30 (Michoacán:Queréndaro)	5	13.2 ± 0.93	(12.5-15.0)	7.9	6.4 ± 0.58	(6.0-7.5)	10.2	6.3 ± 0.40	(6.0-7.0)	7.0
31 (Michoacán:Tarecuato, Tinquindén)	2	12.5 ± 2.00	(11.5-13.5)	11.3	8.3 ± 1.50	(7.5-9.0)	12.8	8.0 ± 1.00	(7.5-8.5)	8.9
32 (Jalisco:Mazamitla)	4	11.6 ± 0.25	(11.5-12.0)	2.1	6.8 ± 0.29	(6.5-7.0)	4.3	6.1 ± 0.25	(6.0-6.5)	4.1
33 (Jalisco:Ciudad Guzmán)	7	13.4 ± 1.54	(11.0-16.5)	15.2	7.8 ± 0.72	(6.5-9.5)	12.2	7.2 ± 0.78	(6.0-9.0)	14.7
34 (Jalisco:Ocotlán)	8	13.8 ± 0.62	(12.5-15.0)	6.4	8.2 ± 0.26	(7.5-8.5)	4.5	7.7 ± 0.32	(7.0-8.5)	6.0
35 (Jalisco:Guadalajara)	10	13.6 ± 0.65	(12.5-16.0)	7.5	8.5 ± 0.38	(7.5-9.5)	7.1	7.8 + 0.37	(7.0-9.0)	7.6
36 (Jalisco:Ameca)	10	14.7 ± 0.75	(13.0-17.0)	8.0	8.7 ± 0.45	(7.5-10.0)	8.2	8.1 ± 0.39	(7.5-9.0)	7.5
37 (Jalisco:Belén de Refugio, Encarnación de Díaz)	5	14.5 ± 1.70	(12.0-17.0)	13.1	9.2 ± 0.87	(8.0-10.5)	10.5	8.2 ± 0.60	(7.5-9.0)	8.2
38 (Jalisco:Comanja de Corona)	8	12.7 ± 0.98	(11.0-15.5)	11.0	7.8 ± 0.46	(7.0-9.0)	8.3	7.3 ± 0.50	(6.0-8.5)	9.8
39 (Guanajuato:Silao)	8	12.8 ± 0.56	(11.5-14.0)	6.2	6.6 ± 0.41	(6.0-7.5)	8.7	6.3 ± 0.33	(5.5-7.0)	7.4
40 (Jalisco:Bolaños)	10	14.5 ± 0.48	(13.5-15.5)	5.3	8.2 ± 0.39	(7.5-9.0)	7.7	8.0 ± 0.41	(7.0-9.0)	8.1
41 (San Luis Potosí: Río Verde)	7	14.4 ± 1.75	(12.0-19.0)	16.2	7.4 ± 0.76	(6.0-9.0)	13.7	7.0 ± 0.72	(6.0-9.0)	13.5
42 (San Luis Potosí: Ahualulco, San Luis Potosí, Villar)	14	12.6 ± 0.73	(10.5-15.0)	10.9	6.6 ± 0.50	(6.0-9.0)	14.0	6.5 ± 0.35	(5.5-8.0)	10.1
43 (Zacatecas:Trancoso, Zacatecas)	6	13.7 ± 0.76	(12.5-14.5)	6.8	8.8 ± 0.92	(7.0-10.0)	14.1	8.4 ± 0.65	(7.0-9.5)	9.5
44 (Zacatecas:Rancho Grande, Sain Alto)	3	15.2 ± 2.03	(13.5-17.0)	11.6	9.3 ± 0.88	(8.5-10.0)	8.1	9.0 ± 0.58	(8.5-9.5)	5.6
45 (Durango:Charro, Durango, Indé, Rodeo)	8	13.7 ± 0.59	(12.5-15.0)	6.1	8.0 ± 0.71	(7.0-10.0)	12.5	7.7 ± 0.68	(6.5-9.5)	12.5
46 (Chihuahua:Parral)	1	13.5			8.5			7.5		

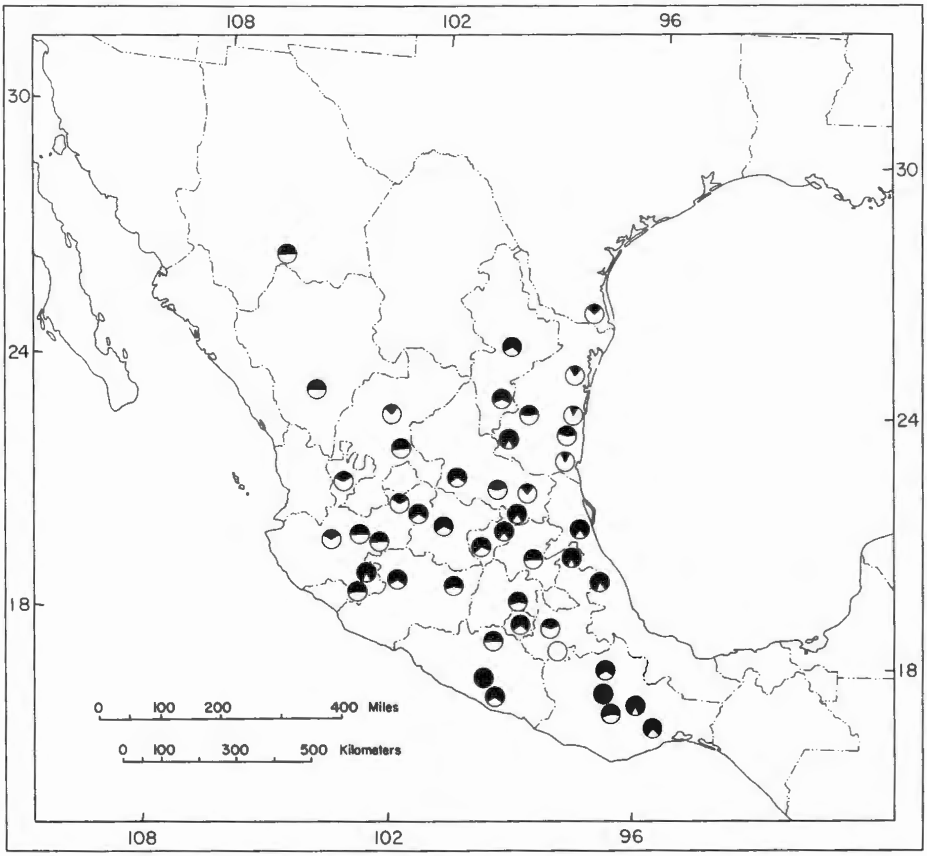


FIG. 16.—Geographic variation in red reflectance of the middorsal coloration of *Liomys irroratus*. The palest sample is represented by an open symbol, the darkest sample by a completely closed symbol, and the remaining samples by symbols that are expressed as a percentage of the difference between these extremes. See Table 8 for areas represented by symbols.

L. guerrerensis from Omilteme, Guerrero. However, the sample from the geographic range of *pullus* (25) had a mean red reflectance of 13.1 (range, 12.0-15.0), which matches closely values for *alleni* in Querétaro and San Luis Potosí and, in fact, is paler than some of them. Compared with the specimens from Omilteme that had a mean of 10.6 for red reflectance with a range of 9.5 to 12.0, they are much paler. Samples from Jalisco had mean values for red reflectance between 12.7 and 14.7.

Generally, there is relatively little variation in color in *Liomys irroratus*; variation that is present seems more related to local variation associated with differences in habitat than to genetic similarities. Essentially this same pattern is repeated for all species of *Liomys*.

Taxonomic Conclusions

Based upon my assessment of geographic variation in *Liomys irroratus*, I have identified seven separate units, which exhibit characteristic evolutionary tendencies and which intergrade (or have intergraded in the recent past) with contiguous units in relatively narrow zones; these seven units are the subspecies of *L. irroratus* here recognized. Four of these units are characterized by relatively large size. The largest individuals of the species and probably the phenetically most distinct occur in the vicinity of Omilteme, Guerrero, to which the trinomial *Liomys irroratus guerrerensis* Goldman, 1911, applies. Another highly distinctive subspecies, *Liomys irroratus bulleri* (Thomas, 1893), occurs in west-central Jalisco and is characterized by large size and a small interparietal bone. The nominate subspecies, *Liomys irroratus irroratus* (Gray, 1868), occupies an area in central Oaxaca southward into the Sierra Madre del Sur of Oaxaca. The last of the subspecies characterized by large size occupies an extensive geographical area northward from Valle de México onto the Mexican Plateau to eastern Jalisco in the west, southern Chihuahua in the northwest, and the Sierra Madre Oriental of Nuevo León in the northeast; the oldest available name for this taxon is *Liomys irroratus alleni* (Coues, 1881). A case could be made for recognition of the populations in western Zacatecas, extreme northern Jalisco, Durango, and southern Chihuahua under the name *Liomys irroratus canus*; however, although these animals are quite large, the change in size from that found in populations in San Luis Potosí forms a gradual cline with no distinct break that can be detected in the material at hand. Therefore, I feel the present arrangement best represents the relationships of these populations.

The three remaining subspecies are characterized by medium to small size. *Liomys irroratus texensis* Merriam, 1902, occurs in the Gulf coastal lowlands of southern Texas, Nuevo León, Tamaulipas, eastern San Luis Potosí, and northern Veracruz. A second subspecies, *Liomys irroratus torridus* Merriam, 1902, occurs south of the Transverse Volcanic Belt in Puebla, Morelos, Guerrero, and northern Oaxaca. In southern and central Jalisco and southern Zacatecas is the medium-sized *Liomys irroratus jaliscensis* (J. A. Allen, 1906).

Liomys irroratus alleni (Coues, 1881)

1881. *Heteromys alleni* Coues, *in* Allen, Bull. Mus. Comp. Zool., 8:187, March.
1911. *Liomys irroratus alleni*, Goldman, N. Amer. Fauna, 34:56, 7 September.
1902. *Liomys canus* Merriam, Proc. Biol. Soc. Washington, 15:44, 5 March; holotype from near Parral, Chihuahua.
1947. *Liomys irroratus pullus* Hooper, J. Mamm., 28:47, 17 February; holotype from Tlalpan, 2250 m., Distrito Federal.
1948. *Liomys irroratus acutus* Hall and Villa-R., Univ. Kansas Publ., Mus. Nat. Hist., 1:253, 26 July; holotype from 2 mi. W Pátzcuaro, 7700 ft., Michoacán.

Holotype.—Probably an adult, sex unknown, skull in skin, MCZ 5889, from Hacienda Angostura, Río Verde [may be near small village of this name, 33 km. NNE Río Verde], San Luis Potosí; obtained on 26 February 1878 by Edward Palmer. Skin in relatively good condition, but condition of skull unknown.

Measurements of holotype.—No measurements are available.

Distribution.—This subspecies has an extensive geographic range on the Mexican Plateau north of the Transverse Volcanic Belt (see Fig. 17). The southern limit of the range of *alleni* is in Tlaxcala, México, Distrito Federal, and northern Michoacán from where it occurs northward into Hidalgo, Querétaro, Guanajuato, northeastern Jalisco, Aguascalientes, Zacatecas, Durango, southern Chihuahua, and San Luis Potosí; specimens referable to *alleni* also are known from the Sierra Madre Oriental of Tamaulipas and Nuevo León.

Comparisons.—*Liomys irroratus alleni* is distinguished from *Liomys irroratus jaliscensis* by its larger size, which is especially noticeable in cranial measurements (compare values for samples 6, 21-25, 29, 30, 33-36 with those of 27, 28 and females from sample 26 in Table 3). None of the qualitative cranial characteristics appear to be sufficiently distinctive to distinguish *alleni* from *jaliscensis*, although samples of the latter do have a somewhat lower percentage of individuals with the posterior termination of the nasals truncate in shape than in most samples of *alleni* (Table 6).

From *Liomys irroratus irroratus*, the subspecies *alleni* can be distinguished by its smaller external size (compare values for samples 6, 21-25, 29, 30, 33-36 with samples 15, 16 in Table 3) and by the terminal shape of the nasals (Table 6). In 62 specimens examined of *irroratus*, only one had the posterior end of the nasals truncate, whereas samples of *alleni* have from 44.4 to 80.0 per cent of the individuals with this characteristic (excepting in sample 24 where only three of 35 individuals have the nasals truncate). Cranial measurements of these two taxa do not appear to be distinctive.

For comparison of *alleni* with *bulleri*, *guerrerensis*, *texensis*, and *torridus*, see accounts of those subspecies.

Remarks.—As understood herein, the name *Liomys irroratus alleni* applies to those populations on the Mexican Plateau north of the Transverse Volcanic Belt that are characterized by large size and a relatively high percentage of individuals with the interparietal bone divided into halves and the posterior termination of the nasals truncate. This subspecies now includes the previously recognized races *acutus*, *canus*, and *pullus*. Hooper and Handley (1948:18-19) pointed out that the population to which Goldman applied the name *alleni* was characterized by no unique feature, but each of the characters attained maximum or minimum development in adjoining areas. Those characters cited (Hooper and Handley, 1948: 18-19) as distinguishing *acutus*, *canus*, and *pullus* were found in my analysis to be non-existent, clinal in nature, or restricted to local situations. For example, all three of these nominal subspecies were supposedly larger than *alleni*. In the univariate analyses, the samples of *acutus* (sample 24) and *pullus* (sample 21) were found to be no larger than *alleni*, but the sample of *canus* (sample 36) was larger. The two intermediate samples (samples 34, 35) form a clinal bridge in many measurements between typical samples of *alleni* (33) and *canus* (36). In the multivariate analysis for males, the two samples 35 and 36 are set off somewhat from the other samples of *alleni*, but in the analysis of females sample 36 fell near 34, 6, and 33. I have interpreted these results to mean that specimens formerly recognized as *L. i. canus* are larger than typical *L. i. alleni* from San Luis Potosí, but that the differences are clinal in nature with no sharp steps in the cline. Therefore, *canus* is best placed as a junior synonym of *alleni*.

Two qualitative cranial characters appear to distinguish the sample of *acutus* (24) from other samples of *alleni*. A much smaller percentage of individuals of *acutus* (5.9 per cent) have a divided interparietal when compared with other samples of *alleni* (15.2 to 50 per cent). Also a much smaller percentage of the specimens of *acutus* (8.6 per cent) have truncate nasals posteriorly than do specimens in other samples of *alleni* (44.4 to 80.0 per cent). However, when all characters are considered at once in the multivariate analysis, the relationship of specimens formerly known as *acutus* is clearly with *alleni*.

In coloration, specimens of *acutus* and *pullus* supposedly are darker than specimens of *alleni* (Hooper and Handley, 1948:18), whereas those of *canus* are somewhat paler (Hooper and Handley, 1948:22). The two samples of *alleni* have quite different mean values for red reflectance, 12.6 and 14.4, and a wide range of individual variation, 10.5 to 19.0. Material from near the type locality of *pullus* has a mean for red reflectance of 13.1, which is darker than in specimens from near the type locality of *alleni* and paler than material from near the city of San Luis Potosí. My sample of material of *acutus* may not be particularly representative of the race, but it averages slightly darker (12.5) in red reflectance than other samples of *alleni* as understood by Hooper and Handley. The two samples of *canus* have mean red reflectance readings (13.5 and 13.7) that are intermediate between the mean values for the two samples of *alleni* from San Luis Potosí. Based on these observations of the dorsal coloration, I see no merit in recognizing more than one race in this complex.

Intergradation between *L. i. alleni* and *L. i. jaliscensis* is evident in specimens from near Lago de Chapala in Jalisco and Michoacán northward through Jalisco into extreme southern Zacatecas. Females in sample 25 from the vicinity of Mazamitla, Jalisco, are somewhat smaller than those from adjacent Michoacán, but clearly they are larger than females from southern Jalisco. In the three-dimensional projection of the multivariate analysis, sample 25 falls at the lower edge of the group that includes other samples of *alleni*, but it is best placed with this group rather than with *jaliscensis*. Specimens in sample 29, especially the males, exhibit intermediate characters between *alleni* and *jaliscensis* in the univariate analysis. In the multivariate analysis, the males fall between *alleni* and *jaliscensis* and could be referred to either; however, the females, although intermediate, fall nearer *alleni*. Examination of the individual specimens in this sample reveals that those from Ocotlán and 10 mi. NE Yahualica in Jalisco are large and are clearly referable to *alleni*, whereas those from 6 mi. N and 4 mi. E Tepatitlán, Jalisco, and 2 mi. SE La Palma, Michoacán, are intermediate in size. Specimens from the vicinity of Tepatitlán are assigned to *alleni* because they have qualitative cranial characters that suggest this relationship (three have the interparietal bone notched posteriorly, and two of three have the interparietal bone divided). The two males from near Zapotlanejo are of interest because they are from the westernmost locality in this area assigned to *alleni*. One specimen is relatively large (greatest length of skull 33.4), but the other is relatively small

(31.8). However, both have cranial characters (interparietal divided and notched, and nasals truncate) that suggest assignment to *alleni* is best until additional material indicates otherwise. The large series of specimens from 4 mi. NE Ocotlán contains only one adult and its cranial characters are inconclusive in indicating relationship with either subspecies. The same is true of specimens from La Palma, Michoacán. I have assigned these to *alleni* because their geographic origin seems to indicate that this was the best course.

Specimens from extreme southern Zacatecas in the vicinity of Santa Rosa evince intergradation between *jaliscensis* and *alleni*. Males from this locality have mean values for seven measurements that are intermediate between values for *alleni* and *jaliscensis* and females are intermediate in five (total length, tail length, greatest length of skull, length of nasals, and depth of braincase for both sexes; hind foot and length of maxillary toothrow for males). Females, although averaging larger than females of *jaliscensis*, had mean values that fall nearer those of *jaliscensis* than *alleni*. In the multivariate analysis, males were intermediate between *alleni* and *jaliscensis*, whereas the females were closer to samples of *jaliscensis*. The cranial characters of this sample also indicate its intermediate nature (Tables 5, 6). I have assigned these specimens to *jaliscensis* because females appear to fit best here and the other evidence would allow assignment to either taxa.

Remains of *Liomys* have been reported previously from San Josecito Cave, near Aramberri, Nuevo León, by Cushing (1945:185) and Jakway (1958:320). Jakway assigned a fragmentary cranium, four right dentaries, and one left dentary available to him to *Liomys irroratus*. The material that I was able to examine in the Vertebrate Paleontology Collection of the Los Angeles County Museum consisted of more than 150 of both right and left dentaries and 66 partial crania. Measurements of the San Josecito Cave material are given in Table 9 along with those of 20 specimens (10 males and 10 females) of *Liomys irroratus alleni* from the general vicinity of the cave. Note that the San Josecito material has a significantly longer maxillary toothrow and right mandibular toothrow than does the Recent material, although it is matched by measurements of other Recent populations of *alleni* from Zacatecas, Durango, and Chihuahua (Table 3). The four other measurements that I was able to take on the cave material, including length of the left mandibular toothrow, showed no significant differences between the two groups. The San Josecito specimens are definitely representatives of *Liomys irroratus* and probably not much different from the Recent representatives of species occurring in the area today. Similar results were obtained by Hooper (1952:58-59, 195), who studied representatives of *Reithrodontomys megalotis* from the cave. Jakway (1958) assigned material of 10 other rodents to Recent species; only one fossil species of rodent, *Orthogeomys onerosus* (Russell, 1960) is recognized from San Josecito Cave material.

Five adult males and eight adult females (nonpregnant) from Zacatecas, San Luis Potosí, and northeastern Jalisco averaged, respectively, 16.8 (16.0-18.0) and 16.0 (15.0-17.0) in length of ear, and 73.7 (70.0-78.8) and 63.7 (48.4-82.0) in weight.

TABLE 9.—*Measurements of* Liomys irroratus *from San Josecito Cave, Nuevo León, and Recent specimens from Nuevo León and Tamaulipas (10 males and 10 females).*

Measurement	Liomys irroratus alleni			San Josecito cave material			t-value	
	N	Mean ± 1 SE	(Range)	N	Mean ± 1 SE	(Range)		
Interorbital constriction	20	8.3 ± 0.08	(7.7-9.1)	26	8.4 ± 0.06	(7.9-9.0)	0.96	ns
Mastoid breadth	20	15.3 ± 0.08	(14.6-16.1)	2	14.7, 15.6		0.37	ns
Length of nasals	20	13.7 ± 0.15	(12.5-15.0)	5	14.0 ± 0.43	(13.2-15.5)	0.71	ns
Length of maxillary toothrow	20	5.4 ± 0.06	(5.0-5.9)	26	5.6 ± 0.05	(5.2-6.0)	2.76	**
Length of right mandibular toothrow	20	5.3 ± 0.06	(4.9-5.9)	20	5.4 ± 0.03	(5.1-5.8)	2.08	*
Length of left mandibular toothrow	20	5.3 ± 0.05	(4.9-5.8)	20	5.4 ± 0.04	(5.1-5.7)	1.60	ns

Specimens examined (707).—AGUASCALIENTES: 3 mi. N Aguascalientes, 2000 m., 1 (MVZ); 18 mi. W, 2 mi. S Aguascalientes, 6000 ft., 1 (KU); 4½ mi. NW Calvillo, 6000 ft., 11 (MVZ); ¼ mi. E state boundary, 8 mi. SW Calvillo, 4 (MVZ); 1 mi. N Chicalote, 1900 m., 2 (MVZ); Chicalote, 1 (USNM); 1 km. S La Labor (9 mi. by road N Calvillo), 1 (MVZ).

CHIHUAHUA: La Cienegilla Springs, 46.9 mi. S Jiménez, 2 (TTU); near Parral (31 miles northwest of Parral according to Goldman, 1951:124), 8 (USNM); 5 mi. E Parral, 5700 ft., 1 (KU); Santa Rosalía, 1 (USNM).

DISTRITO FEDERAL: Cerro Xaltepec, 1½ mi. NNW Zapotitlán, 2380 m., 2 (1 KU, 1 UNAM); Ciudad Universitaria, 1 (UNAM); Contreras, 2600 m., 3 (UMMZ); Pedregal de San Angel, 3 (ENCB); San Gerónimo, 2400 m., 27 (UMMZ); San Gregorió Altapulco, 2270 m., 1 (KU); ¼ mi. NNE San Mateo Xalpa, 2390 m., 1 (KU); 200 m. N San Mateo Xalpa, 1 (UNAM); Tlalpan, 16 (2 FMNH, 11 UMMZ, 3 USNM); ½ km. N Xochitepec, 2250 m., 1 (UNAM).

DURANGO: 5½ mi. NNW Canatlán, 6400 ft., 1 (MSU); 1 mi. N Chorro, 6450 ft., 1 (KU); 8 mi. NW Durango, 6200 ft., 1 (KU); Durango, 1 (USNM); Indé, 5 (USNM); Navarro, 1 (UA); Río Nazas, 10 mi. NNW Rodeo, 2 (KU); Río Sestín, 4 (AMNH); Rosario, 6 (AMNH); 3 mi. SE Tepehuanes, 5840 ft., 6 (MSU).

GUANAJUATO: Acámbaro, 1 (USNM); Moroleón, 1 (USNM); Salvatierra, 5775 ft., 1 (KU); 5 km. N San José, 3 (WBC); Silao, 8 (USNM).

HIDALGO: 10 mi. NW Actopan, 6000 ft., 2 (MSU); 2 km. E Actopan, 2 (ENCB); 12 km. S, 2 km. E Actopan, 8200 ft., 1 (KU); 1 km. N Epazoyucan, 2550 m., 3 (ENCB); Ixmiquilpan, 5550 ft., 1 (KU); 6 mi. S Ixmiquilpan, 1 (ENCB); Maguey Verde, 8½ mi. NE Zimapán, 7100 ft., 1 (MVZ); Marqués, 2 (USNM); San Agustín, 1100 m., 3 (UMMZ); Tula, 2050 m., 3 (1 FMNH, 2 USNM); Zacualtipán, 1800 m., 4 (UMMZ); Zimapán, 6 (3 UMMZ, 3 USNM).

JALISCO: 2 mi. S Ayo el Chico, 5400 ft., 3 (KU); Belén de Refugio, 5700 ft., 5 (KU); 4½ mi. NE Comanja de Corona, 8000 ft., 10 (KU); 9 mi. N Encarnación, 1900 m., 12 (11 MVZ, 1 UNAM); 5½ mi. N, 2 mi. W Guadalupe de Victoria, 1 (MSU); Huascato, 3 (ENCB); 3 mi. S Huejúcar, 5900 ft., 1 (KU); 5 mi. NE Huejuquilla, 6200 ft., 3 (KU); 1 mi. S Jalostotitlán, 5700 ft., 1 (KU); 7 mi. N Lago de Moreno, 1 (UNAM); 2 mi. WNW Lagos de Moreno, 6370 ft., 1 (KU); 1½ mi. N Mazamitla, 5 (UMMZ); ½ mi. NW Mazamitla, 2 (UMMZ); 4 mi. W Mazamitla, 6600 ft., 3 (KU); 3 mi. WSW Mazamitla, 1 (KU); 4 mi. NE Ocotlán, 5050 ft., 26 (24 KU, 2 MSU); 2 mi. WNW Ocotlán, 5000 ft., 4 (KU); Ocotlán, 15 (USNM); 1 mi. S Ocotlán, 5000 ft., 1 (KU); 6 mi. N, 4 mi. E Tepatitlán, 6400 ft., 2 (KU); 2 mi. S, ½ mi W Tepatitlán, 1 (KU); 3 mi. E Unión de San Antonio, 6100 ft., 4 (KU); 10 mi. NE Yahualica, 5 (KU); 2 mi. E Zapotlanejo, 2 (KU).

MEXICO: Atlacomulco, 2500 m., 2 (UMMZ); 1.1 km. N Barrientos, 2300 m., 1 (ENCB); Cerro La Caldera, 11 mi. SE Mexico City, 2350 m., 7 (3 KU, 4 UNAM); 3 km. E, 2 km. S Chilpa, 2270 m., 4 (ENCB); 3.5 km. W Ecatepec, 2500 m., 3 (ENCB); Hacienda Cordoba, 2600 m., 1 (UMMZ); 23 km. E México, 7500 ft., 20 (2 KU, 18 TCWC); 4 km. SSE San Rafael, 2460 m., 1 (KU); Temascaltepec, 4 (UMMZ); Tenancingo, 2050 m., 2 (FMNH); 5 mi. S, 1 mi. W Texcoco, 7350 ft., 1 (KU); 1 km. E Teotihuacán, 2420 m., 3 (ENCB); 2 km. NW Tlalnepantla, 2300 m., 2 (ENCB); 4 km. ENE Tlalmanalco, 2290 m., 4 (2 KU, 2 UNAM); 2 km. NE Tlalpitzahuac, 1 (KU); 3 km. N Valle de Bravo, 4 (UNAM); 1½ mi. S Valle de Bravo, 6050 ft., 3 (KU); 3 mi. ENE Zoquiapan, 9200 ft., 1 (MSU).

MICHOACAN: 3 mi. S Carapan, 6900 ft., 2 (MSU); 4 mi. S Cuitzeo, 1800 m., 19 (UMMZ); 9 km. W Jacona, 4 (ENCB); 4 km. SW Jacona, 1 (ENCB); 13 km. SW Jacona, 2 (ENCB); 2 mi. SE La Palma, SE side Lago de Chapala, 3 (KU); 2 mi. E La Palma, SE side Lago de Chapala, 1 (MSU); 12 km. W Morelia, 1 (UNAM); 15 mi. E Morelia, jct. of highway 4 and road to Tzitzio, 2150 m., 1 (UMMZ); 8 mi. NE Pátzcuaro, 2 (MVZ); 3 mi. NW Pátzcuaro, 6700 ft., 1 (MVZ); 2 mi. W Pátzcuaro, 6700-7700 ft., 7 (MVZ); Pátzcuaro, 6 (2 FMNH, 1 MCZ, 2 UMMZ, 1 USNM); 5 mi. S Pátzcuaro, 7800 ft., 11 (4 MSU, 7 MVZ); Queréndaro, 5 (USNM); 11 mi. W Quiroga, 1 (UMMZ); Tancítaro, 6000 ft., 1 (FMNH); 4½ mi. NE

Tarecuato, 6600 ft., 1 (KU); 1 mi. N Tinqüindín, 6300 ft., 1 (KU); Zamora, 3 (USNM); 3 mi. E Zamora, 5480 ft., 1 (MSU); 10 km. E Zamora, 3 (ENCB).

NUEVO LEON: Aramberri, 3600 ft., 1 (KU); 1 km. SW Aramberri, 3600 ft., 1 (KU); 5 mi. W Ascención, 6500 ft., 1 (KU); Ibarilla, 35 mi. S Linares, 3000 ft., 7 (KU); Iturbide, Sierra Madre Oriental, 5000 ft., 5 (KU); Ojo de Agua, 1 (FMNH); Pablillo, 38 km. W, 28 km. S Linares, 7400 ft., 3 (KU); 1½ mi. N Zaragoza, 4500 ft., 3 (KU); 1 mi. S Zaragoza, 4600 ft., 1 (KU).

QUERETARO: Cadereyta, 2100 m., 4 (UMMZ); Jalpan, 11 (USNM); 5 mi. NE Pinal de Amoles, 6500 ft., 1 (MSU); Pinal de Amoles, 9 (3 UMMZ, 6 USNM); 15 km. N Querétaro, 2 (TCWC); 6 mi. E Querétaro, 7400 ft., 5 (KU); 6 mi. E Querétaro, 6450 ft., 1 (MSU); Tequisquiapan, 1 (USNM): Tolimán, 1700 m., 15 (UMMZ).

SAN LUIS POTOSI: Ahualulco, 6 (USNM); Alvarez, 8 (4 AMNH, 4 MCZ); 2 km. NE Arriaga, 2 (LSU); Bledos, 20 (LSU); Cerro Campanario, 1 (LSU); Cerro Peñon Blanco, 7750 ft., 1 (LSU); Hacienda Angostura, 3 (1 MCZ, 2 USNM); Hacienda Capulín, 3 (LSU); Hacienda La Parada, 3 (USNM); Jesús María, 2 (USNM); Paso de San Antonio, 1 (LSU); 8 mi. SW Ramos, 6700 ft., 8 (KU); Río Verde, 13 (1 LSU, 12 USNM); 1½ mi. E Río Verde, 3 (LSU); San Carlos, 1 (AMNH); 10 mi. NE San Luis Potosí, 3 (2 KU, 1 MSU); 11 km. S, 3½ km. E Santa María del Río, 1800 m., 1 (ENCB); Villar, 18 (3 LSU, 15 USNM).

TAMAULIPAS: Jaumave, 49 (3 FMNH, 23 KU, 22 UMMZ, 1 USNM); Miquihauna, 3 (USNM); Nicolás, 56 km. NW Tula, 5500 ft., 6 (KU); 16 mi. N, 6 mi. W Palmillas, 5500 ft., 1 (KU); 14 mi. N, 6 mi. W Palmillas, 5500 ft., 2 (KU).

TLAXCALA: 5 mi. W Ciudad Tlaxcala, 3 (YPM).

VERACRUZ: 10 km. SW Jacales, 6500 ft., 2 (KU).

ZACATECAS: Berriozábal, 4 (USNM); 4 mi. NNW Chalchihuites, 7000 ft., 3 (CAS); Hacienda San Juan Capistrano, 2 (USNM); 13 mi. N Jalpa, 5000 ft., 1 (KU); 3 mi. SW Jalpa, 4600 ft., 3 (KU); 1 mi. NE Noria de Angeles, 1 (CAS); 10 mi. N Rancho Grande, 6200 ft., 11 (MSU); 5 mi. SE Río Grande, 6360 ft., 1 (MSU); Río Nieves, 1 mi. N Rancho Grande, 1 (KU); 2 mi. W Saín Alto, 6900 ft., 2 (KU); 2 mi. ESE Trancoso, 1 (KU); 7 mi. SE Trancoso, 1 (KU); Valparaíso, 20 (USNM); 9 mi. W Zacatecas, 7800 ft., 1 (CAS); 5 mi. NW Zacatecas, 7600 ft., 3 (KU); 8 mi. SE Zacatecas, 7225 ft., 4 (KU).

Additional records.—DURANGO: 9 mi. N Durango (Baker and Greer, 1962:104). JALISCO: Encarnación de Díaz (Grant, 1947:8; Johnson, 1962:417). NUEVO LEON: San Francisco (Koestner, 1941:12).

Marginal records (localities in italics are not plotted on Fig. 17 because undue crowding of symbols would have resulted).—CHIHUAHUA: Santa Rosalía; La Cienegilla Springs, 46.9 mi. S Jiménez. DURANGO: Indé; Río Nazas, 10 mi. NNW Rodeo. ZACATECAS: 5 mi. SE Río Grande, 6360 ft.; 10 mi. N Rancho Grande, 6200 ft.; Río Nieves, 1 mi. N Rancho Grande; 5 mi. NW Zacatecas, 7600 ft. SAN LUIS POTOSI: 8 mi. SW Ramos, 6700 ft.; Cerro Peñon Blanco; Ahualulco; Villar; San Carlos. TAMAULIPAS: Nicolás, 56 km. NW Tula, 5500 ft. NUEVO LEON: 5 mi. W Ascención, 6500 ft.; Pablillo, 38 km. W, 28 km. S Linares, 7400 ft. San Francisco; *Ojo de Agua*; Iturbide, Sierra Madre Oriental, 5000 ft.; Ibarilla, 35 mi. S Linares, 3000 ft.; *Aramberri, 3600 ft.*; *1 1/2 mi. N Zaragoza, 4500 ft.*; 1 mi. S Zaragoza, 4600 ft. TAMAULIPAS: Jaumave. San Luis Potosí: 1½ mi. E Río Verde; Hacienda Capulín. QUERETARO: Jalpan. HIDALGO: Maguey Verde, 8½ mi. NE Zimapán, 7100 ft.; Zacualtipan. VERACRUZ: 10 km. SW Jacales, 6500 ft. HIDALGO: 1 km. N Epazoyucan, 2550 m. TLAXCALA: 5 mi. W Ciudad Tlaxcala. MEXICO: 4 km. SSE San Rafael, 2460 m. DISTRITO FEDERAL: San Gregorió Altapulco; *200 m. N San Mateo Xalpa.* MEXICO: Tenancingo, 2050 m.; Temascaltepec. MICHOACAN: 5 mi. S Pátzcuaro, 7800 ft.; Tancítaro, 6000 ft.; 1 mi. N Tinqüindín, 6300 ft. JALISCO: *3 mi. WSW Mazamitla*; 4 mi. W Mazamitla, 6600 ft. MICHOACAN: *2 mi. SE La Palma, SE side Lago de Chapala.* JALISCO: 1 mi. S Ocotlán, 5000 ft.; *2 mi. WNW Ocotlán, 5000 ft.;* 2 mi. E Zapotlanejo; 2 mi. S, ½ mi. W Tepatitlán; 10 mi. NE Yahualica. ZACATECAS: 3 mi. SW Jalpa, 4600 ft. JALISCO: 3 mi. S Huejúcar, 5900 ft.; 5 mi. NE Huejuquilla, 6200 ft. ZACATECAS: Hacienda San Juan Capistrano; 4 mi. NNW

Chalchihuites, 7000 ft. DURANGO: Durango; 8 mi. NW Durango; 3 mi. SE Tepehuanes, 5840 ft.; Navarro. CHIHUAHUA: near Parral.

Liomys irroratus bulleri (Thomas, 1893)

1893. *Heteromys bulleri* Thomas, Ann. Mag. Nat. Hist., ser. 6, 11:330, April.
1911. *Liomys bulleri*, Goldman, N. Amer. Fauna, 34:61, 7 September.

Holotype.—Adult female, skin in alcohol with skull removed, BMNH 93.3.6.39, from La Laguna, Sierra de Juanacatlán, Jalisco; obtained in December 1892 by A. C. Buller. Skin in alcohol in good condition; skull in good condition excepting a lower incisor broken.

Measurements of holotype.—Greatest length of skull, 34.1; zygomatic breadth, 16.7; interorbital constriction, 8.6; mastoid breadth, 15.5; length of nasals, 13.4; length of rostrum, 15.3; length of maxillary toothrow, 5.9; depth of braincase, 10.0; interparietal width, 7.4; interparietal length, 3.9.

Distribution.—Known only from the vicinity of La Laguna and Soyatlán del Oro in west-central Jalisco (see Fig. 17).

Comparisons.—*Liomys irroratus bulleri* can be distinguished from the subspecies *jaliscensis*, *texensis*, and *torridus* by its larger external and cranial size (see Table 3). From the remaining subspecies of *irroratus* (*alleni*, *guerrerensis*, and *irroratus*) as well as those mentioned above, *bulleri* is distinguished by its small triangular or subtriangular interparietal bone. The small size of the interparietal is matched in only one sample of *alleni* (specimens formerly allocated to *acutus*), but in these specimens the interparietal is semicircular in shape (Hall and Villa-R., 1948:254).

Remarks.—*Liomys irroratus bulleri* is a large-sized subspecies known only from a restricted area in west-central Jalisco. It is potentially in contact only with the medium-sized *L. i. jaliscensis* to the east in central Jalisco. Until the present study, *bulleri* had been considered a monotypic species closely related to *irroratus*. The characters described by Goldman as distinctive of *bulleri* were its small and subtriangular interparietal bone and rounded termination of the nasals. The latter character is definitely not unique to *bulleri* because at least some individuals in all samples of *Liomys irroratus* exhibit this condition. The small size of the interparietal is rather unique for the species, but it is matched in a population in Michoacán (sample 24). Furthermore, because the size and shape of the interparietal bone is highly variable in *Liomys irroratus*, as it is in other species in the genus, I do not believe it is a character upon which specific distinction can be based. I have no evidence in my limited material to indicate intergradation of *bulleri* with *jaliscensis*, but the two taxa have a relationship that is similar to that between *L. i. torridus* and *L. i. irroratus*. On the basis of my findings, the relationships of *bulleri* are best expressed by considering it as a distinct subspecies of *Liomys irroratus* rather than retaining it as a monotypic species.

In the multivariate analysis, samples 37 and 38 are relatively far removed from other samples of *irroratus* in the three-dimensional plot, especially in the second principal component. In the second component, the two most heavily weighted characters by far are length and width of the interparietal.

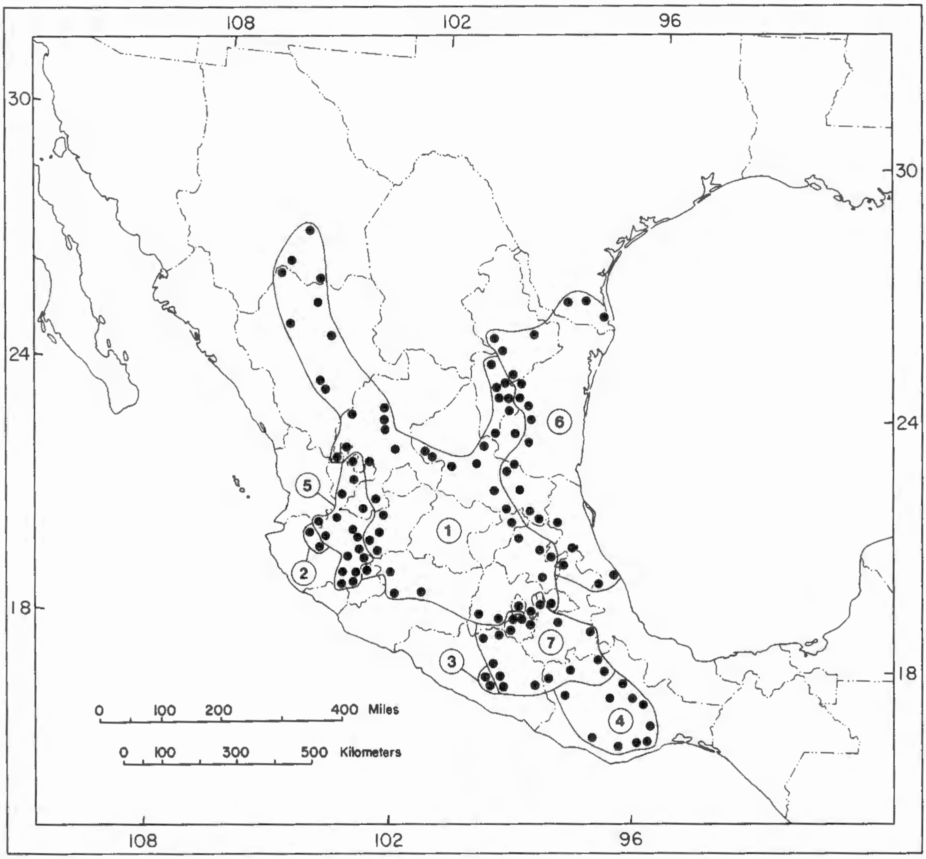


FIG. 17.—Geographic distribution of subspecies of *Liomys irroratus:* 1, *L. i. alleni*; 2, *L. i. bulleri*; 3, *L. i. guerrerensis*; 4, *L. i. irroratus*; 5, *L. i. jaliscensis*; 6, *L. i. texensis*; 7, *L. i. torridus*.

Until the present study, *Liomys irroratus bulleri* was known by only two specimens from the type locality, La Laguna, Jalisco. However, five specimens in the University of Arizona collection from the vicinity of Soyatlán del Oro, Jalisco (sample 37), also appear to be referable to this taxon. The one adult female from this area is large as are the holotype and a topotype and all of the specimens have small interparietal bones (besides the adult female in Table 3, two subadult males and a subadult female had the following measurements: interparietal width, 7.0, 7.0, 6.4 and interparietal length 3.6, 3.3, 3.5). Specimens from the vicinity of Soyatlán del Oro extend the geographical range of *bulleri* approximately 60 kilometers to the southeast. The adult female from Soyatlán del Oro weighed 51 grams.

Specimens examined (7).—JALISCO: La Laguna, Sierra de Juanacatlán, 2 (1 BMNH, 1 USNM); Rancho de Colomo, 3 km. E Soyatlán del Oro, 1 (UA); 3 km. N Soyatlán del Oro, 2 (UA); 5 km. W Soyatlán del Oro, 1 (UA); 5 km. S Soyatlán del Oro, 1 (UA).

Marginal records.—Jalisco: La Laguna, Sierra de Juanacatlán; *3 km. N Soyatlán del Oro*; *Rancho de Colomo, 3 km. E Soyatlán del Oro*; 5 km. S Soyatlán del Oro; *5 km. W Soyatlán del Oro.*

Liomys irroratus guerrerensis Goldman, 1911

1911. *Liomys guerrerensis* Goldman, N. Amer. Fauna, 34:62, 7 September.

Holotype.—Subadult female, skin and skull, USNM 127523, from Omilteme, Guerrero; obtained 17 May 1903 by E. W. Nelson and E. A. Goldman. Skin in good condition; skull with broken zygoma.

Measurements of holotype.—Total length, 255.0; length of tail, 127.0; length of hind foot, 34.0; greatest length of skull, 33.3; interorbital constriction, 8.6; mastoid breadth, 15.8; length of nasals, 12.5; length of rostrum, 14.9; length of maxillary toothrow, 6.0; depth of braincase, 9.2; interparietal width, 8.5; interparietal length, 3.6.

Distribution.—Pacific slope of the Sierra Madre del Sur of Guerrero in the vicinity of the type locality (see Fig. 17).

Comparisons.—*Liomys irroratus guerrerensis* can be distinguished from all other races of *Liomys irroratus* by its larger size, both externally and cranially (compare values of sample 39 with others in Table 3). In addition, the sample of *guerrerensis* is darker dorsally than any other sample of the species. Compared with adjacent samples of *L. i. torridus* (17, 18), *guerrerensis* has a much larger percentage of individuals with the posterior margin of the interparietal notched and the posterior termination of nasals rounded (Tables 5, 6).

Remarks.—Until the present study, *guerrerensis* has been considered a monotypic species, although it was long recognized as being closely related to *irroratus*. However, my study of variation within the species *irroratus* and the relationship of *guerrerensis* with *irroratus* has convinced me that this relationship is best expressed by placing *guerrerensis* as a race of *irroratus*. The range of *guerrerensis* is confined to the wet montane forests of the Pacific slope of Sierra Madre del Sur in the vicinity of Omilteme, Guerrero. The nearest known localities of occurrence of other populations of *irroratus* (subspecies *torridus*) are approximately 20 miles to the east in the vicinity of Chilpancingo, Guerrero.

The relationship between *L. guerrerensis* and *L. irroratus* was investigated using discriminant function analysis. Because only seven specimens of *guerrerensis* were available for this analysis, the characters were divided into two sets and discriminant multipliers were generated for both sets. Two discriminant scores were produced for each specimen and these were plotted on a scatter diagram (Fig. 18). The reference sample of *irroratus* was taken from sample 18, which is composed of specimens from north of the Río Balsas in Guerrero. Discriminant multipliers produced using the reference samples of *irroratus* and *guerrerensis* (Table 10) were used to produce discriminant scores for specimens from the vicinity of Chilpancingo, Guerrero. The discriminant scores for the specimens from Chilpancingo also are plotted on Fig. 18. For the first set of characters (total length, length of tail, length of hind foot, greatest length of skull, length of rostrum and length of maxillary toothrow) the reference sample of *guerrerensis* had discriminant scores that ranged from 44.13 to 46.68, whereas the reference sam-

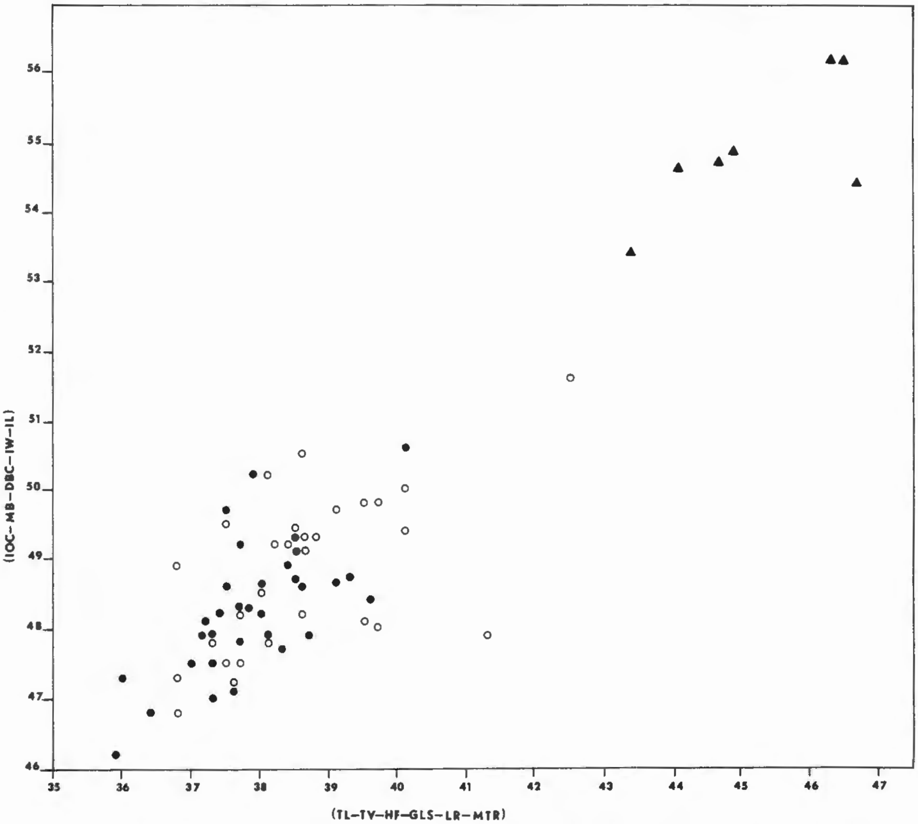


FIG. 18.—Scatter diagram based upon discriminant scores generated by a discriminant function analysis comparing *Liomys irroratus torridus* and *Liomys irroratus guerrerensis*. Two analyses had to be performed because only seven specimens of *guerrerensis* were available (characters used in each are indicated at the left and bottom of the diagram). The reference sample of *torridus* (closed circles) was based upon specimens from north of the Río Balsas in Guerrero and the reference sample of *guerrerensis* (closed triangles) was based upon specimens from the vicinity of Omilteme, Guerrero. The specimens in the test sample (open circles) were from south of the Río Balsas in Guerrero in the vicinity of Chilpancingo. See text for discussion.

ple of *irroratus* had scores ranging from 35.85 to 40.06; for the second set of characters (interorbital constriction, mastoid breadth, depth of braincase, interparietal width, interparietal length), the reference sample of *guerrerensis* had discriminant scores of 53.37 to 56.23, whereas *irroratus* had values of 46.23 to 50.64.

When specimens from Chilpancingo were plotted on the scatter diagram, most of the specimens fell within the range of variation of the *Liomys irroratus* reference sample; however, at least two fell outside the range and one of these is nearly perfectly intermediate between the *guerrerensis* and *irroratus* samples. The intermediate specimen (MVZ 106515) from Chilpancingo had discriminant scores of

TABLE 10.—*Discriminant multipliers resulting from a discriminant function analysis comparing* Liomys irroratus torridus *and* Liomys irroratus guerrerensis. *Characters were divided into two sets because of the small sample size of* guerrerensis.

First set of characters		Second set of characters	
Measurements	Discriminant multipliers	Measurements	Discriminant multipliers
Total length	0.060	Interorbital constriction	0.516
Length of tail	−0.037	Mastoid breadth	1.913
Length of hind foot	0.181	Depth of braincase	2.054
Greatest length of skull	0.362	Interparietal width	−0.368
Length of rostrum	−0.321	Interparietal length	0.559
Length of maxillary toothrow	3.219		

42.49 and 51.60 and the other specimen (FMNH 47559), also from Chilpancingo, had scores of 41.32 and 47.92. The latter has a relatively low score for the second set of characters, owing to a relatively narrow interorbital constriction and a shallow depth of braincase. A third specimen (UMMZ 104999) from Chilpancingo is of interest, but was not plotted on Fig. 18 because it lacks measurements for total length and length of tail. However, if the means for sample 17 are used for these missing measurements, values of 40.17 and 53.18 are obtained; the score for the first set of characters probably is low because the means used underestimate the original measurements of this specimen.

The possibility of some intergradation between *torridus* and *guerrerensis* as well as biosystematic information that no differences were found between *irroratus* and *guerrerensis* in bacular morphology, karyotypic morphology, or pterygoid structure clearly indicate that the two taxa are closely related. On the basis of this evidence, I feel justified in recognizing *guerrerensis* as a subspecies of *irroratus*.

Three adult males and three nonpregnant, adult females from the vicinity of Omilteme, Guerrero, had the following measurements, respectively: length of ear, 18, 19, 17, 19, 19, 18.5; weight, 81.7, 89.6, 71.7, 76.6, 65.2, 58.8.

Specimens examined (18).—GUERRERO: 15 km. SW Chilpancingo, 9000 ft., 2 (TCWC); 1 mi. NW Omilteme, 7260 ft., 2 (USNM); Omilteme, 7300 ft., 8 (2 ENCB, 3 KU, 1 MVZ, 2 USNM); 2 mi. E Omilteme, 6600 ft., 5 (KU); 1 mi. SW Omilteme, 1 (USNM).

Marginal records.—GUERRERO: 1 mi. NW Omilteme; *2 mi. E Omilteme*; 15 km. SW Chilpancingo; *1 mi. SW Omilteme*.

Liomys irroratus irroratus (Gray, 1868)

1868. *Heteromys irroratus* Gray, Proc. Zool. Soc. London, p. 205, May.
1911. *Liomys irroratus*, Goldman, N. Amer. Fauna, 34:53, 7 September.
1868. *Heteromys albolimbatus* Gray, Proc. Zool. Soc. London, p. 205, May; lectotype from La Parada, Oaxaca (Thomas, 1927:552).
1956. *Liomys irroratus yautepecus* Goodwin, Amer. Mus. Novit., 1757:7, 8 March; holotype from Rancho Sauce, San Pedro Jilotepec, 5000 ft., Oaxaca.

Holotype.—Subadult of unknown sex, skin and skull, BMNH 59.7.10.2, from Oaxaca; obtained on an unknown date by A. Sallé. Goldman (1911:53-54) considered material from the city of Oaxaca as typical of *irroratus* and the type locality is herewith restricted to Oaxaca, Oaxaca. Skin in rather poor condition with the tail broken off and attached to the skin by a string. The left zygomatic arch is broken and the cranium lacks the posterior portion including the interparietal, right bulla, and occipital and basicranial elements.

Measurements of holotype.—Interorbital constriction, 9.1; length of nasals, 12.5; length of rostrum, 15.2; length of maxillary toothrow, 6.3; mastoid breadth, 15.2 ±.

Distribution.—This subspecies is confined to central and south-central Oaxaca (Fig. 17). It occurs in mountainous areas and in the Valley of Oaxaca, but is not found on the coastal plain of southern Oaxaca where it is replaced by *Liomys pictus*.

Comparisons.—The nominate subspecies can be distinguished from the races *jaliscensis, texensis,* and *torridus* by larger external and cranial size—compare values for sample 15 and 16 (*irroratus*) with samples 26 to 28 (*jaliscensis*), to and 7 to 10 (*texensis*), and 11 to 14 and 17 to 20 (*torridus*) in Table 3. In addition, samples of *irroratus* have a large percentage of individuals with the posterior margin of the nasals emarginate (see Table 6) and a small percentage with a truncate margin, whereas the reverse is true in samples of *jaliscensis*. Most samples of *jaliscensis* have a somewhat greater percentage of individuals with the interparietal divided than do samples of *irroratus* (see Table 5), but it would be impossible to separate the two subspecies on the basis of this character.

Cranial characters of *irroratus* that tend to distinguish it from *texensis* are a greater incidence of notching of the posterior margin of the interparietal, a greater incidence of divided interparietal, and a lesser incidence of truncated posterior margin of the nasals (Tables 5, 6). The qualitative cranial differences that distinguish *irroratus* and *torridus* are essentially the same as those that distinguish *irroratus* from *texensis,* although the percentage of individuals that exhibit notching of the posterior margin of the interparietal is not so different when populations of *irroratus* and *torridus* (especially sample 14) are compared as when populations of *irroratus* and *texensis* are compared.

For comparisons of *irroratus* with *alleni, bulleri,* and *guerrerensis* see the accounts of those subspecies.

Remarks.—This large-sized race was the first member of the genus, as it now is understood, to be described. In 1868, J. E. Gray described *Heteromys irroratus* based on a single specimen from the state of Oaxaca, and in the same paper he described *Heteromys albolimbatus* on the basis of two specimens from La Parada, Oaxaca. Since Goldman's revision of the genus, *albolimbatus* has been considered a junior synonym of *irroratus,* a conclusion with which I agree. It is of interest to note that Gray's description of *albolimbatus* includes the following statement: "This species is known from the others by the greater softness of the fur, the greater slenderness of the hair, and the abundance of the elongated under-fur. . . . " Examination of the lectotype and lectoparatype in the British Museum revealed that these specimens were juveniles still in juvenile pelage, which accounts for the unusual nature of the pelage described by Gray.

Goodwin (1956*a*:7) described a subspecies, *L. i. yautepecus*, on the basis of a single specimen from San Pedro Jilotepec in the coastal mountains of southern Oaxaca. Later, he (Goodwin, 1969:148) placed *yautepecus* as a junior synonym of *irroratus*. In the preceding univariate and multivariate analyses, sample 15 includes specimens believed to be typical of *irroratus* and sample 16 includes specimens from the range of *yautepecus*. The two samples constantly fell near each other, indicating little difference between them, and I, therefore, agree with Goodwin's conclusion that *yautepecus* should be considered a junior synonym of *irroratus*.

The only subspecies of the species with which *Liomys irroratus irroratus* is potentially in contact is *torridus* in northern Oaxaca and central Guerrero, but I have seen no specimens from northern Oaxaca that I would judge to be intergrades between the two. Specimens from the vicinity of Chilpancingo, Guerrero, have been assigned to *irroratus* by some authors (see Hooper and Handley, 1948: 11); although these specimens average somewhat larger than other samples of *torridus*, their affinities are clearly with them. The exact relationship of these Guerreran specimens and with *L. i. irroratus* will not be clear until material becomes available from the mountainous areas of southeastern Guerrero and west-central Oaxaca.

The average weights of seven adult males and five adult females (nonpregnant) of the subspecies were, respectively, 65.6 (54.8-76.6) and 54.6 (48.0-62.3); the mean length of ear for these same individuals was 17.4 (16.0-19.0) and 18.8 (17.0-21.0).

Specimens examined (136).—OAXACA: Benito Juárez Nat'l Park, S side Cerro San Felipe, 5500 ft., 1 (MVZ); Cerro San Felipe, 4 (1 UMMZ, 1 UNAM, 2 USNM); Chivaguela, 1 (AMNH); Ejutla, 1400 m., 3 (UMMZ); 8 mi. SSW Juchatengo, 6300 ft., 8 (MSU); La Cima, Oaxaca-Puerto Escondido Road, 5800 ft., 6 (CAS); La Parada, 2 (BMNH); 2 mi. SE Matatlán, 5950 ft., 4 (KU); Miahuatlán, 1100 m., 8 (UMMZ); 3 mi. W Mitla, 3 (KU); Monte Alban, 4 mi. SW Oaxaca, 6000 ft., 15 (10 MSU, 5 MVZ); Mt. Zempoaltepec, 5 (USNM); 7 mi. NNE Oaxaca, 1 (UMMZ); 6 mi. NNE Oaxaca, 6000 ft., 3 (UMMZ); Oaxaca, 36 (14 FMNH, 1 UMMZ, 21 USNM); 3 mi. ESE Oaxaca, 5 (KU); 4 mi. ESE Oaxaca, 5050 ft., 1 (KU); 10 mi. SE Oaxaca, 5000 ft., 1 (CAS); Km. 177.2 Oaxaca-Puerto Escondido Road, 5800 ft., 1 (CAS); Km. 183 Oaxaca-Puerto Escondido Road, 6000 ft., 1 (CAS); Río Molino, Oaxaca-Puerto Angel Road, 7100 ft., 4 (CAS); Río Jalatengo, Km. 178 Oaxaca-Puerto Angel Road, 4275 ft., 3 (CAS); San Lucas Ixcotepec, 1 (AMNH); San Pedro Jilotepec, 5000 ft., 1 (AMNH); Santa Catalina Quień, 1 (AMNH); Santa Mańa Candelaria, 5 (AMNH); Santo Tomás Quień, 1 (AMNH); Santo Tomás Teipan, 1 (AMNH); Sierra Juárez, Ixtlán, 1 (UMMZ); Sola de Vega, 1(UMMZ); 1 mi. E Tlacolula, 5500 ft., 5 (UMMZ); unspecified locality, 1 (BMNH); Yalalag, 1 (USNM); Zapotitlán, 1 (AMNH).

Additional records.—OAXACA (Goodwin, 1969:148): San Andrés Chicahuaxtla; San Miguel Suchitepec; Santo Tomás Ocotepec; Yaitepec.

Marginal records.—OAXACA: Sierra Juárez; Yalalag; Mt. Zempoaltepec; San Pedro Jilotepec; Zapotitlán; Santa Mańa Candelaria; Río Jalatengo, Km. 178 Oaxaca-Puerto Angel Road, 4275 ft.; 8 mi. SSW Juchatengo, 6300 ft.; San Andrés Chicahuaxtla; 7 mi. NNE Oaxaca.

Liomys irroratus jaliscensis (J. A. Allen, 1906)

1906. *Heteromys jaliscensis* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 22:251, 25 July.
1911. *Liomys irroratus jalicensis* [*sic*], Goldman, N. Amer. Fauna, 34:60, 7 September.

Holotype.—Adult male, skin and skull, AMNH 26325, from Las Canoas, 7000 ft., Jalisco; obtained on 6 August 1905 by J. H. Batty. Both zygomatic arches are broken and the pterygoid processes are missing, but otherwise the skull is in good condition; the skin is in fairly good condition.

Measurements of holotype.—The external measurements were recorded in inches. Greatest length of skull, 31.6; interorbital constriction, 8.0; mastoid breadth, 14.1; length of nasals, 11.6; length of rostrum, 13.4; length of maxillary toothrow, 5.2; depth of braincase, 9.2; interparietal width, 8.7; interparietal length, 3.7.

Distribution.—The subspecies *jaliscensis* is known from southern, central, and northern Jalisco and extreme southern Zacatecas and Nayarit (see Fig. 17).

Comparisons.—From *Liomys irroratus texensis*, the subspecies *jaliscensis* is distinguished by its larger, longer cranium (measurements such as greatest length of skull, length of rostrum, and length of maxillary toothrow) and by its proportionately shorter nasals, which average less than those of *texensis* (compare samples 26-28 with 1-5, 7-10 in Table 3). Samples of *texensis* tend to have a greater percentage of individuals with the posterior margin of the interparietal unnotched than do samples of *jaliscensis*, whereas samples of *jaliscensis* have a greater percentage of individuals with the interparietal bone divided than do samples of *texensis* (see Table 5).

Liomys irroratus jaliscensis can be distinguished from *Liomys irroratus torridus* by its somewhat larger overall size (compare samples 26-28 with 12-14, 17-20 in Table 3), but the difference is not so great as that between *jaliscensis* and *alleni* or *torridus* and *alleni*. Samples of *jaliscensis* have a much greater percentage of individuals with the interparietal divided than do samples of *torridus* (see Table 5). It should be pointed out that these three subspecies—*jaliscensis*, *texensis*, and *torridus*—are geographically isolated from each other; they represent populations of small-to-medium-sized individuals that are separated by populations of larger-sized individuals.

For comparisons of *jaliscensis* with *alleni*, *bulleri*, *guerrerensis*, and *irroratus*, see the accounts of those subspecies.

Remarks.—The specimens from sample 26 present a rather difficult situation taxonomically in that the males fall with samples of *alleni* in the multivariate analysis, whereas females fall with samples of *jaliscensis* (Figs. 12-15). Because the holotype and paratypes of *jaliscensis* are included in sample 26, the application of the name *jaliscensis* itself needs to be scrutinized. In the univariate analysis (Fig. 9 and Table 3), it can be seen that males of sample 26 definitely fall with samples of *alleni* in at least seven measurements (total length, length of tail, length of hind foot, greatest length of skull, zygomatic breadth, interorbital constriction, and mastoid breadth), but in at least four other measurements (length of nasals, length of rostrum, length of maxillary toothrow, and depth of braincase) the mean values for males are smaller than values for *alleni* and are near those for males of other samples (27, 28) of *jaliscensis.* With the possible exceptions of zygomatic breadth and interorbital constriction, females from locality 26 have mean values that are similar to those of females from samples 27 and 28 and are much smaller than those for females of *alleni.*

I have applied the name *jaliscensis* to specimens from southern, central, and northern Jalisco and extreme southern Zacatecas. I decided upon this course of action for several reasons, not the least of which is that it conveys a certain stability to the taxonomy of mice in this area. One of the alternatives to the recognition of *jaliscensis* would be to place it in the synonymy of *alleni* and describe a new race from central Jalisco where more "typical" specimens of this small-sized subspecies are to be found; I have chosen not to follow this course of action. One good reason for recognition of *jaliscensis* is that females from southern Jalisco resemble females in other samples that are included in this taxon. Another reason is that the male holotype and paratypic males are relatively small, being of a size similar to males from central Jalisco (greatest length of skull of two paratypes, 32.4 and 32.3). One thing that weakens this argument is the fact that many of the localities included in this sample lie between the type locality and the central Jaliscan localities.

The only possible explanation I can offer for this situation (large males resembling *alleni* and proportionately smaller females resembling samples from central Jalisco) is that some sort of character displacement is occurring in this population, because *Liomys pictus* in known from this area and, in fact, was taken along with *irroratus* at one of the included localities. A similar situation is seen in the zone of overlap between *Liomys pictus* and *Liomys salvini* in southeastern Oaxaca and northwestern Chiapas; in these species only the males evinced the effects of the character displacement (see section on specific relationships). This leaves unanswered the question of why the effects of character displacement are not seen in central Jalisco where *irroratus* and *pictus* also occur together.

Specimens from the eastern margin of the geographic range of *jaliscensis* are of interest because of possible intergradation with *alleni.* Four adult specimens from 3 mi. NW Chapala, however, are small-sized and in all characters appear to be more or less typical of *jaliscensis.* One specimen from 7 km. SE Tonalá is a juvenile and the one from 8 mi. E Tizapán is a rather small subadult. These specimens have been assigned to *jaliscensis* mainly because their geographic origin suggested this would be the best arrangement at present. Additional material may show these suppositions to be erroneous. For additional discussion of intergradation between *alleni* and *jaliscensis* in eastern Jalisco and southern Zacatecas, see the account of *alleni.*

There appears to be some confusion about the exact location of the type locality of *jaliscensis,* Las Canoas, Jalisco, in Allen's (1906) paper in which the race was described. On page 238, he stated that Las Canoas was "on the tableland, about 40 miles west of Tuxpan, at an altitude of about 7000 feet" and at the bottom of the page and the top of the next he stated that collections were made "in southern Jalisco, a little west of Tuxpan." Elsewhere in the paper, such as in the account of *Platogeomys gymnurus,* the location is given as "Las

Canoas, near Zapotlan." Finally in the description of *Heteromys jaliscensis* the placement of Las Canoas is given as "about 20 miles west of Zapotlan, Jalisco," and it is this location that is cited by most subsequent authors. The location of Las Canoas at either 40 miles west of Tuxpan or 20 miles west of Zapotlan [=Ciudad Guzmán] seems to me to be highly unlikely especially in the case of the former. Both of these localities are west of other localities where *jaliscensis* is known to occur. It seems more likely to me that the type locality is a small town by the name, shown on some recent maps, that is 10 km. NW Tuxpan and 10 km. SSW Ciudad Guzmán. This locality is near several others from which *Liomys irroratus* is known and is on the tableland east of the highland of Sierra Nevada de Colima on which Tuxpan and Ciudad Guzmán are situated.

The ear of 10 adult males and females from central Jalisco averaged, respectively, 15.4 (14.5-17.0) and 15.0 (14.5-16.0) in length. The weights of these same individuals averaged 54.2 (46.0-69.6) and 44.0 (30.8-52.2).

Specimens examined (358).—JALISCO: 7 km. S Acatlán, 9 (ENCB); 3 mi. N Amatitán, 4050 ft., 1 (KU); 2 mi. N Amatitán, 4050 ft., 9 (KU); 2 mi. NNW Amatitán, 4000 ft., 2 (KU); 1½ mi. WNW Amatitán, 4100 ft., 6 (KU); Amatitán, 4050 ft., 11 (KU); 3 mi. NNW Ameca, 4300 ft., 6 (KU); 7 mi. W Ameca, 4000 ft., 23 (UMMZ); 6 mi. W Ameca, 4300 ft., 1 (UMMZ); Ameca, 10 (USNM); 1 mi. SW Ameca, 4000 ft., 36 (KU); 2 mi. SW Ameca, 4000 ft., 6 (KU); 1 mi. SSE Ameca, 4000 ft., 31 (KU); Arroyo de Gavalan, 4 (AMNH); Atemajac, 9 (USNM); 5 mi. W Atenquique, 6500 ft., 1 (MSU); Barranca de Tule, Sierra Nayarit, 2 (USNM); 6 mi. ENE Bolaños, 5350 ft., 6 (KU); 4 mi. ENE Bolaños, 4400 ft., 1 (KU); Bolaños, 2800 ft., 3 (KU); 1 mi. E Bolaños, 3350 ft., 1 (KU); 3 mi. NW Chapala, 5100 ft., 8 (UMMZ); 10 mi. W Ciudad Guzmán, 6500 ft., 4 (1 UA, 3 UMMZ); 2 mi. N Ciudad Guzmán, 14 (KU); 9/10 mi. S Ciudad Guzmán, 5050 ft., 2 (KU); 3½ mi. W Etzatlán, 4400 ft., 1 (KU); Etzatlán, 1 (USNM); 2 6/10 mi. E Etzatlán, 4300 ft., 13 (KU); 3 mi. N Guadalajara, 5100 ft., 6 (KU); 2 mi. N, ½ mi. W Guadalajara, 2 (KU); 5 mi. S Guadalajara, 1 (UA); 8 mi. S Guadalajara, 5050 ft., 2 (UMMZ); 20 km. S Guadalajara, 1 (ENCB); 13 mi. S, 15 mi. W Guadalajara, 17 (KU); 19 mi. SW Guadalajara, 1 (MSU); 27 mi. S, 12 mi. W Guadalajara, 3 (KU); 2½ mi. ENE Jazmín, 6800 ft., 1 (KU); 9 mi. NW Jocotepec, 5240 ft., 2 (MSU); La Primavera, 12 mi. W Guadalajara, 5600 ft., 1 (UMMZ); Las Canoas, 10 (AMNH); 3 mi. W La Venta, 3 (KU); 2 mi. NW Magdalena, 4500 ft., 1 (KU); 1 mi. NW Mezquitic, 5000 ft., 2 (KU); N slope Nevado de Colima, 8000 ft., 1 (LACM); 6 mi. W San Marcos, 5400 ft., 6 (KU); 3 mi. ENE Santa Cruz de las Flores, 9 (KU); Sierra Nevada, 1 (USNM); 1 mi. NE Tala, 4400 ft., 4 (KU); 3 mi. W Tala, 4300 ft., 5 (KU); 4½ mi. W Teuchitlán, 4300 ft., 11 (KU); 8 mi. E Tizapán, 1 (MSU); 7 km. SE Tonalá, 1 (ENCB); 3½ mi. NW Villa Guerrero, 5500 ft., 1 (KU); 3 mi. N Villa Guerrero, 5600 ft., 2 (KU); 4½ mi. W Villa Guerrero, 5200 ft., 1 (KU); 3½ mi. WNW Zapoltitic, 5100 ft., 17 (KU); 2 7/10 mi. WNW Zapoltitic, 5000 ft., 3 (KU); Zapotlán, 2 (USNM).

ZACATECAS: 8 mi. S Moyahua, 5600 ft., 9 (CAS); 1 mi. N Santa Rosa, 3600 ft., 10 (MSU).

Additional records.—JALISCO: Arroyo de Plantanar (J. A. Allen, 1906:251); 11 mi. SE Guadalajara (Levine *et al.*, 1958:295); 21 mi. SW Guadalajara (Twente and Baker, 1951: 120). NAYARIT: Ojo de Agua (J. A. Allen, 1906:251).

Marginal records.—JALISCO: 1 mi. NW Mezquitic, 5000 ft.; 3 mi. N Villa Guerrero, 5600 ft. ZACATECAS: 1 mi. N Santa Rosa; *8 mi. S Moyahua*. JALISCO: Atemajac; 7 km. SE Tonalá; 3 mi. NW Chapala; 8 mi. E Tizapán; 2 mi. N Ciudad Guzmán; *Zapotlán* [=Ciudad Guzmán]; *9/10 mi. S Ciudad Guzmán*; *2 7/10 mi. WNW Zapotiltic*; Las Canoas; 5 mi. W Atenquique; *2 1/2 mi. ENE Jazmín, 6800 ft.*; 10 mi. W Ciudad Guzmán, 6500 ft.; 27 mi. S, 12 mi. W Guadalajara; *7 km. S Acatlán*; *2 mi. SW Ameca, 4000 ft.*; 7 mi. W Ameca, 4000 ft. NAYARIT: Ojo de Agua. JALISCO: 6 mi. W San Marcos, 5400 ft.; 2 mi. NW Magdalena, 4500 ft.; Bolaños, 2800 ft.

Liomys irroratus texensis Merriam, 1902

1902. *Liomys texensis* Merriam, Proc. Biol. Soc. Washington, 15:44, 5 March.
1911. *Liomys irroratus texensis*, Goldman, N. Amer. Fauna, 34:59, 7 September.
1911. *Liomys irroratus pretiosus* Goldman, N. Amer. Fauna, 7 September; holotype from Metlaltoyuca, Puebla.

Holotype.—Adult female, skin and skull, USNM 58670, from Brownsville, Cameron Co., Texas; obtained on 19 February 1894 by J. A. Loring. Skin and skull in good condition, except lacrimal bones missing.

Measurements of holotype.—Total length, 231; length of tail, 114; length of hind foot, 30; greatest length of skull, 31.0; zygomatic breadth, 14.5; interorbital constriction, 8.0; mastoid breadth, 14.1; length of nasals, 12.8; length of maxillary toothrow, 5.2; depth of braincase, 8.6; interparietal width, 7.0; interparietal length, 4.0.

Distribution.—Gulf coastal lowlands of Texas, Tamaulipas, Nuevo León, San Luis Potosí, Veracruz, and Puebla (see Fig. 17). The localities in Texas mark the northeastern limit of distribution for the species.

Comparisons.—From *Liomys irroratus alleni*, the subspecies *texensis* can be distinguished by its much smaller size, both externally and cranially (compare values for samples 1-5, 7-10 with 6, 22, 33, 34 in Table 3). The only qualitative cranial character that tends to distinguish these two subspecies is the division of the interparietal bone, which occurs in low frequency in populations of *texensis*, excepting those in Veracruz (7, 10), but in more than 30 per cent of the individuals in adjacent populations of *alleni*.

For comparisons of *texensis* with *bulleri*, *guerrerensis*, *irroratus*, *jaliscensis*, and *torridus*, see the accounts of those subspecies.

Remarks.—This small- to medium-sized subspecies is confined to the Gulf coastal lowlands of northeastern México and southern Texas. Intergradation is evident between *texensis* and *alleni* for a considerable distance along the eastern foothills of the Sierra Madre Oriental and the eastern edge of the Mexican Plateau. Specimens from the vicinity of Monterrey (previously assigned to *alleni* by Goldman, 1911:57) and from west of Allende and Linares in Nuevo León are somewhat larger than specimens from the lowlands to the east in Tamaulipas, but they are considerably smaller than specimens of *alleni* from contiguous populations (sample 6). In Tamaulipas, specimens of *texensis* revealing intergradation with *alleni* were examined from Rancho Santa Rosa, Hidalgo, Villa Mainero (previously assigned to *alleni* by Alvarez, 1963:433), several localities to the west of Ciudad Victoria, El Carrizo, and El Encino. In San Luis Potosí, the zone of intergradation is not well delimited because specimens are lacking from critical areas. Specimens from the lowlands and eastern edge of the Plateau in the vicinity of El Salto and Ciudad del Maíz fit best with other populations of *texensis*, whereas specimens from near Río Verde are clearly *alleni*. Also in Veracruz, Hidalgo, and Querétaro the width and exact location of the zone of intergradation are not clear, although specimens from Jalpan, Querétaro, are much smaller than others of *alleni* and could be as easily assigned to one subspecies as the other on the basis of size. However, because a high percentage (45.4) of these individuals have an interparietal bone that is divided, I have assigned them to *alleni*.

The specimens from Metlaltoyuca, Puebla, the type locality of *Liomys irroratus pretiosus* described by Goldman (1911:58), are, I believe, intergrades between *texensis* and *alleni*. Their relatively large size is explained by that fact. In the univariate and multivariate analyses, those specimens previously assigned to *pretiosus* clearly fall with typical *texensis*; therefore, I regard *pretiosus* as a junior synonym of *texensis*. It is true that specimens from the vicinity of the type locality of *pretiosus* have the anterior portion of the nasals somewhat more inflated than is typical of *texensis*, but I do not believe this is sufficient to warrant recognition of the race in light of the numerous similarities with *texensis*.

Some geographic variation was noted within the subspecies *texensis*. Specimens from northern samples in Texas and northern Tamaulipas (1, 2) averaged somewhat larger than specimens from other samples, although those from central Veracruz (10) were relatively large. The smallest specimens of *texensis*, on the average, were from the vicinity of Ebano, San Luis Potosí (8). Samples from along the Rio Grande in Texas and Tamaulipas (1, 2) also differed from others in having a much higher frequency of individuals in which the posterior margin of the interparietal bone was unnotched. On the other hand, the two samples from Veracruz (7, 10) had a higher frequency (37.5 and 26.1, respectively) of individuals with the interparietal bone divided in half.

A specimen (skull only) in the University of Michigan, Museum of Zoology (105005), which was acquired from the Cleveland Museum of Natural History, was supposedly collected at Ingram, Kerr County, Texas in 1914. This locality has not been plotted on Fig. 17 because the place is approximately 260 miles to the north-northwest of the nearest known locality and in a general habitat quite different from that along the Gulf coast of Texas. Also, relatively extensive trapping has been done in Kerr County by several mammalogists over the years and no other specimens have been obtained. It seems best to consider that this specimen was mislabeled, unless additional material from the area becomes available. Aside from this specimen, the northernmost record for the subspecies is 10 mi. NW Raymondville in Willacy County (see Blair, 1949:201-202; 1952:241).

Koopman and Martin (1959:2, 6) reported a subfossil maxillary fragment of *Liomys irroratus* from a small cave 1 km. S Aserradero del Paraiso, Tamaulipas. From late Pleistocene deposits in the nearby Cueva del Abra, Tamaulipas, Dalquest and Roth (1970:226) recorded 49 jaws assignable to *irroratus*. Although I have not examined this material, it is probably referable to *L. i. texensis*, which commonly occurs in these areas today.

Ten adult males and 10 nonpregnant, adult females from coastal regions of central and northern Tamaulipas had ears that averaged, respectively, 14.9 (13.5-17.0) and 15.2 (13.0-18.0) in length and weights that averaged 48.1 (37.9-58.0) and 42.2 (38.0-50.0).

Specimens examined (800).—NUEVO LEON: Cerro de la Silla, 1 (USNM); China, 1 (USNM); 20 km. NW General Terán, 900 ft., 5 (UMMZ); 8 mi. W Linares, 1 (MWU); 2½ mi. W Linares, 1650 ft., 5 (KU); 7 mi. S, 16 mi. W Linares, 2200 ft., 1 (KU); 10 km. SSE Linares, 1 (KU); 20 km. NW Montemorelos, 1 (TCWC); Montemorelos, 4 (USNM); Monterrey, 9 (USNM); 3 mi. SW Monterrey, 1965 ft., 5 (KU); Río Ramas, 4 mi. W Allende, 1700 ft., 3 (KU); San Pedro Santiago, 1 (MCZ).

PUEBLA: Metlaltoyuca, 7 (USNM); Pahuatlán, 1100 m., 2 (UMMZ); 1 km. NW Zihuateutla, 1 (KU).

SAN LUIS POTOSI: 4 mi. SSW Ajinche, 1 (LSU); 1.5 mi. S Ajinche, 2 (LSU); 20 mi. W Antiguo Morelos (Tamaulipas), 2 (MVZ); Apetsco, 2 (LSU); 10 mi. E, 2 mi. N Ciudad del Maíz, 1 (KU); 4 km. NE Ciudad Valles, 3 (KU); Ebano, 5 (LSU); 14 km. SW Ebano, 10 (LSU); 10 mi. WSW Ebano, 7 (LSU); 19 km. SW Ebano, 8 (LSU); 22 km. SW Ebano, 8 (7 LSU, 1 ROM); 1 mi. E El Abra, 1 (KU); El Bañito, 1 (FMNH); 3 mi. W El Naranjo, 1300 ft., 1 (MSU); 0.5 mi. E El Sabinito, 1200 ft., 1 (LSU); El Salto, 22 (18 AMNH, 3 LSU, 1 UNAM); Hacienda Limón, 10 mi. W Ebano, 1 (LSU); Huichihuayán, 1 (LSU); Mirador del Moctezuma, 6 km. N Tamazunchale, 350 m., 1 (UNAM); 10 km. E Platanito, 16 (LSU); Puerto del Lobos, 1 (LSU); Río Axtla, 3 km. W Axtla, 1 (KU); 1 mi. N Tamazunchale, 700 ft., 5 (MSU); Tamazunchale, 1 (AMNH); 3 km. S Tamazunchale, 7 (MWU); 2½ mi. N Tamuín, 1 (LSU); 3 mi. E Tamuín, 2 (LSU); Tanimul, 10 mi. ESE Valles, 2 (AMNH); 4 km. N Valles, 13 (LSU); 3 km. N Valles, 19 (LSU); 30 km. W Valles, 1 (MWU); Valles, 3 (USNM).

TAMAULIPAS: Acuña, Sierra de Tamaulipas, 800 m., 7 (UMMZ); Altamira, 9 (1 KU, 8 USNM); 1 mi. S Altamira, 3 (KU); 2½ mi. S Altamira, 2 (TTU); 2½ mi. SE Altamira, 1 (TTU); 10 km. N Antiguo Morelos, 22 (MWU); 8 km. NE Antiguo Morelos, 500 ft., 2 (KU); Antiguo Morelos, 9 (UMMZ); 3½ mi. S Antiguo Morelos, 900 ft., 2 (MSU); near Bagdad, 3 (USNM); Cañada del Abra, 15 km. SSW Ciudad Mante, 2 (UNAM); Ciudad Mante, 1 (MWU); Km. 577 carretera Ciudad Mante y Ciudad Victoria, 1 (ENCB); 29 mi. N Ciudad Victoria, 3 (MVZ); 36 km. N, 10 km. W Ciudad Victoria [1 km. E El Barretal on Río Purificación], 1 (KU); 15 mi. N Ciudad Victoria, 2 (KU); 15 km. N Ciudad Victoria, 1 (MWU); 12 km. N Ciudad Victoria, 1 (WBC); 70 km. S Ciudad Victoria and 2 km. W El Carrizo, 6 (5 KU, 1 UNAM); Cueva del Abra, 12 km. S Ciudad Mante, 6 (UNAM); Cueva de Quintero, 12 km. S Quintero, 250 m., 24 (UNAM); Ejido Santa Isabel, 2 km. W Pan American Highway, 3 (KU); 3 mi. W El Carrizo, 1500 ft., 1 (UMMZ); 53 km. N El Limón, and 12 km. S Río Guayalejo, 4 (KU); 5 mi. NE Gómez Farías, 2 (UMMZ); Gómez Farías, 10 (AMNH); Hacienda Acuña, 2650 ft., 7 (MSU); Hacienda San José, near Soto la Marina, 2 (LSU); Hacienda Santa Engracia, 3 (FMNH); Hidalgo, 2 (USNM); 4 mi. N La Pesca, 5 (KU); 8 km. NW La Pesca, 2 (TNHC); 7 mi. W La Pesca, 25 ft., 10 (MSU); 6 mi. W La Pesca, 3 (MSU); 7 km. SW La Purísima, 1 (KU); Marmolejo, San Carlos Mts., 5 (UMMZ); Matamoros, 19 (USNM); 5.7 mi. S Matamoros, 3 (MVZ); Mulato, 1 (UMMZ); Pano Ayuctle, 5 mi. NE Gómez Farías, 2 (AMNH); Rancho Milagro, 11 mi. SW Cruillas, 1 (UMMZ); Rancho Pano Ayuctle, 25 mi. N El Mante, thence 3 km. W highway, 300 ft., 1 (KU); Rancho Pano Ayuctle, 6 mi. N Gómez Farías, 300 ft., 8 (KU); Rancho Pano Ayuctle, 3 mi. NE Gómez Farías, 2 (CAS); Rancho Santa Rosa, 25 km. N, 13 km. W Ciudad Victoria, 260 m., 2 (KU); 24 mi. ESE Reynosa, 5 (MVZ); Río Corona, 19 mi. E Ciudad Victoria, 7 (MCZ); near headwaters of Río Sabinas, 8 km. W, 10 km. N El Encino, 1 (KU); Río Soto la Marina, Rancho Santa Ana, 8 mi. SW Padilla, 4 (MCZ); 7 km. S, 2 km. W San Fernando, 8 (7 KU, 1 UNAM); San José, San Carlos Mts., 1 (UMMZ); Sierra de Tamaulipas, 10 mi. W, 2 mi. S Piedra, 1200 ft., 37 (KU); Sierra Madre Oriental, 5 mi. S, 3 mi. W Ciudad Victoria, 1900 ft., 18 (KU); Soto la Marina, 35 (25 KU, 6 LSU, 4 USNM); 10 mi. NW Tampico, 1 (KU); 7 km. N Tampico, 2 (KU); Victoria, 6 (USNM); Villa Mainero, 1700 ft., 3 (KU).

VERACRUZ: 1 km. ENE Coyutla, 5 (KU); 3 km. W Gutiérrez Zamora, 300 ft., 7 (KU); Ixcatepec, 70 km. NW Tuxpan, 3 (KU); La Mar, 20 ft., 1 (KU); Miahuapa, 8 km. N Coyutla, 80 m., 6 (KU); Miahuapa (La Tulapilla), 15 km. NNE Coyutla, 80 m., 3 (KU); Nautla, 10 (UMMZ); Ozulama, 500 ft., 3 (KU); Papantla, 4 (USNM); 4 km. E Papantla, 400 ft., 1 (KU); 9 km. E Papantla, 300 ft., 6 (KU); Piedras Clavadas, 75 km. NW Tuxpan, 2 (KU); Platón Sánchez, 800 ft., 4 (KU); Potrero Llano, 350 ft., 4 (KU); 3 km. SW San Marcos, 2 (KU); 5 mi. S Tampico (Tamaulipas), 4 (KU); 12½ mi. N Tihuatlán, 300 ft., 8 (KU); 4 km. W Tlapacoyan, 1700 ft., 7 (KU); 35 km. NW Tuxpan, 2 (KU); 25 km. NW Tuxpan, 2 (KU);

17 km. NW Tuxpan, 1 (KU); 15 km. NW Tuxpan, 1 (KU); 14 km. NW Tuxpan, 1 (KU); 6 km. N Tuxpan, 1 (KU); 5 km. NE Tuxpan, 1 (KU); 4 km. NE Tuxpan, 3 (KU).

TEXAS: Alamo, Hidalgo Co., 3 (LSU); 8 mi. S Alamo, Hidalgo Co., 1 (USNM); 4 mi. N Brownsville, Cameron Co., 1 (TTU); 10 mi. W Brownsville, Cameron Co., 2 (LSU); Brownsville, Cameron Co., 116 (33 AMNH, 8 FMNH, 2 KU, 12 LACM, 2 LSU, 8 MCZ, 1 SDNHM, 2 TCWC, 1 UCLA, 47 USNM); 20 mi. E Brownsville on Rt. 4, Cameron Co., 1 (UNM); 17 mi. NW Edinburg, Hidalgo Co., 5 (TNHC); 6 mi. N, 1 mi. W Edinburg, Hidalgo Co., 1 (MWU); Elsa, Hidalgo Co., 2 (ROM); Fort Brown, Cameron Co., 1 (USNM); Ingram, Kerr Co., 1 (UMMZ) (not mapped, see text); Laguna Atascosa, *ca.* 8 mi. NW Bayside, Cameron Co., 1 (LSU); Laguna Atascosa, 10 mi. E Rio Hondo, Cameron Co., 1 (LSU); Lomita Ranch, Hidalgo Co., 4 (USNM); 6 mi. S McAllen, Hidalgo Co., 27 (TNHC); 5 mi. S Mission, Hidalgo Co., 1 (LSU); no specific locality, Cameron Co., 2 (SDNHM); 10 mi. NW Raymondville, Willacy Co., 4 (TNHC); San Benito, Cameron Co., 1 (LACM).

Additional records.—SAN LUIS POTOSI: 10 mi. W Ebano (Dalquest, 1953:121); Tamuín (Dalquest, 1953:122). TAMAULIPAS: 2 mi. S Ciudad Mante (Ingles, 1959:394); Mesa de Llera (Hooper, 1953:5); 3 mi. W Soto la Marina (Hooper, 1953:5). VERACRUZ: El Tajín (Ingles, 1959:394). TEXAS: Bentsen State Park, Hidalgo Co. (Hudson and Rummel, 1966: 346); Noriega Wildlife Refuge, 4.5 mi. NW Brownsville, Cameron Co. (Eads *et al.*, 1965:18).

Marginal records.—TEXAS: 10 mi. NW Raymondville, Willacy Co.; Laguna Atascosa, 10 mi. E Rio Hondo, Cameron Co., thence southward along the coast. VERACRUZ: Nautla; 4 km. W Tlapacoyan. PUEBLA: Pahuatlán, 1100 m.; Metlaltoyuca. VERACRUZ: Platón Sánchez. SAN LUIS POTOSI: 3 km. S Tamazunchale; Apetsco; 30 km. W Valles; Puerto del Lobos; El Salto. TAMAULIPAS: near headwaters of Río Sabinas, 8 km. W, 10 km. N El Encino; Sierra Madre Oriental, 5 mi. S, 3 mi. W Ciudad Victoria, 1900 ft.; Rancho Santa Rosa, 25 km. N, 13 km. W Ciudad Victoria, 260 m.; 7 km. SW La Purísima; Villa Mainero, 1700 ft. NUEVO LEON: 7 mi. S, 16 mi. W Linares, 2200 ft.; Río Ramas, 4 mi. W Allende, 1700 ft.; 3 mi. SW Monterrey; *Monterrey*; China. TEXAS: 17 mi. NW Edinburg, Hidalgo Co.

Liomys irroratus torridus Merriam, 1902

1902. *Liomys torridus* Merriam, Proc. Biol. Soc. Washington, 15:45, 5 March.
1911. *Liomys irroratus torridus*, Goldman, N. Amer. Fauna, 34:55, 7 September.
1902. *Liomys torridus minor* Merriam, Proc. Biol. Soc. Washington, 15:45, 5 March; holotype from Huajuapan de León, Oaxaca.
1903. *Heteromys exiguus* Elliot, Field Columb. Mus., Zool. Ser., 3:146, 20 March; holotype from Puente de Ixtla, Morelos.

Holotype.—Adult female, skin and skull, USNM 69645, from Cuicatlán, Oaxaca; obtained on 14 October 1894 by E. W. Nelson and E. A. Goldman. Skin and skull in good condition.

Measurements of holotype.—Total length, 242.0; length of tail, 134.0; length of hind foot, 28.0; greatest length of skull, 30.3; zygomatic breadth, 14.2; interorbital constriction, 7.9; mastoid breadth, 14.0; length of nasals, 11.6; length of rostrum, 13.6; length of maxillary toothrow, 4.5; depth of braincase, 8.9; interparietal width, 8.9; interparietal length, 3.5.

Distribution.—The geographic range of *Liomys irroratus torridus* lies south of the Transverse Volcanic Belt of México in Puebla, Morelos, northern Oaxaca, and northern and central Guerrero.

Comparisons.—When values for external and cranial measurements of samples of *torridus* (12-14, 18-20) are compared with those for *texensis* (1-5, 7-10), *torridus* is found to average smaller than *texensis* in some cranial measurements, but usually the difference is slight (Table 3). A slight difference is also observed when both of these subspecies are compared with samples of *jaliscensis*, but all three are geographically isolated from each other. Samples of *texensis*, excepting those from Veracruz (7, 10), have a greater percentage of individuals with the posterior termination of the nasals truncate in shape than do those of *torridus* (Table 6).

From *Liomys irroratus alleni*, the subspecies *torridus* is distinguished by its much smaller size, both externally and cranially (compare values of samples 12-14, 18-20 with 21-24, 29, 30, 33-36 in Table 3). Furthermore, samples of *torridus* have a relatively small percentage of individuals (when compared with samples of *alleni*) that have the interparietal bone divided and the posterior termination of the nasals truncated (Tables 5, 6).

For comparison of *torridus* with *bulleri*, *guerrerensis*, *irroratus*, and *jaliscensis*, see the accounts of those subspecies.

Remarks.—The subspecies *torridus* is composed of individuals of medium to small size for the species. It occurs in the dry areas of Puebla south of the Transverse Volcanic Belt, in northern Oaxaca, Morelos, and northern and central Guerrero. The distribution in Guerrero is of special interest; in this state, the population is split and one segment is presently isolated from the other. In the uplands north of the Río Balsas *Liomys irroratus* is the only species of the genus present and this segment is continuous with other populations of *torridus* in Morelos. As the elevation decreases in the descent into the valley of the Río Balsas, *L. irroratus* is replaced by *L. pictus* at about 2000 feet. I have seen specimens of both species from the vicinities of Iguala and Los Sabinos on the north edge of the valley and from near Zumpango on the south edge. The population of *torridus* in the highlands south of the valley of the Balsas, therefore, is isolated from populations to the north of the valley by the intervening populations of *L. pictus* and is evidently contiguous with other *torridus* in northern Oaxaca and southern Pueblo along the south side of the Río Mexcala as is indicated by specimens from Ayotzinapa, Sochi, Tlalixtaquilla, and Tlapa.

Specimens from the vicinity of Chilpancingo (sample 17) average somewhat larger than individuals from north of the Río Balsas (sample 18) in some measurements (total length, greatest length of skull, mastoid breadth, and length of rostrum). In these measurements, specimens from sample 17 tend to be intermediate between *irroratus* and *torridus*, but in all other measurements they clearly fall with the northern Guerreran material. Sample 17 has a greater percentage of individuals with the interparietal divided than do other samples of *torridus* and a slightly smaller percentage than do samples of *irroratus*. The relationships of Guerreran specimens from south of the Río Balsas is clearly with other populations of *torridus*. The characters in which this population has diverged from *torridus* may have resulted from some genetic influence from populations of *irroratus* in Oaxaca; however, this will be verified only when material becomes available from the mountainous areas of southeastern Guerrero and west-central Oaxaca.

Populations of *Liomys irroratus torridus* and *Liomys irroratus alleni* intergrade along the southern slope of the Transverse Volcanic Belt in Morelos and

Puebla, and in the lower country of eastern Puebla. As pointed out in the univariate and multivariate analyses, the sample from the vicinity of Tehuacán in eastern Puebla (11) averages intermediate in size between samples of *alleni* to the northwest and samples of *torridus* to the west and south. The intermediate size of specimens from this area was pointed out earlier by Hooper and Handley (1948: 12). The percentage of individuals with the interparietal bone divided in sample 11 is similar to that of populations of *torridus* and unlike that of *alleni*, but the percentage of individuals with the posterior margin of the nasals truncated is intermediate between the values for *torridus* and *alleni* (Tables 5, 6). I have assigned this series of specimens to *torridus* because it fell in the multivariate analysis with the other samples of that subspecies rather than with the group containing the samples of *alleni*; in analysis for males and females, sample 11 fell relatively near sample 17, which also has been included in *torridus*. Specimens from 7 mi. S and 3 mi. E Puebla and from San Martín in northern Puebla were also judged to be intergrades between *alleni* and *torridus*. These specimens are intermediate in size between the two—values for two males from near Puebla and a female from San Martín, respectively, were total length, 245.0, 234.0, 232.0; greatest length of skull, 33.4, 31.6, 32.0; mastoid breadth, 14.6, 14.1, 14.7—but only one of six specimens had the nasals truncate in shape posteriorly and only one had the interparietal divided, thus suggesting assignment to *torridus*.

In Morelos, specimens from the vicinities of Tepoztlán and Huitzilac are somewhat larger than those examined from elsewhere in the state, but I do not believe they should be included with populations from the Valley of Mexico as was done by Davis and Russell (1954:73) with specimens from 2 mi. SW Tepoztlán. The largest individual from these localities is a female from 1.5 mi. SE Huitzilac (TCWC 4733) with a greatest length of skull of 32.5, which is clearly below the average, 33.3, of female *alleni* from the Valley of Mexico; I have assigned these specimens, therefore, to *torridus*. A subadult from 20 km. NE Cuautla (TCWC 4768) is assigned to *torridus* on the basis of qualitative cranial characters—undivided interparietal bone and emarginate posterior margin of nasals. An adult female (FMNH 55985) from Tenancingo, México, a short distance west of several localities in Morelos, has been assigned to *alleni* because of its large size (greatest length of skull, 33.4; mastoid breadth, 15.1).

The status of *Liomys irroratus minor* was questioned earlier by Hooper and Handley (1948:13) and my analysis reveals that *minor* is, indeed, indistinguishable from *torridus*. In the multivariate analysis (see Figs. 12-15), samples from the vicinity of the type localities of *minor* (sample 13) and *torridus* (sample 14) are placed close to each other and I can see no possible justification in this material for recognition of two races. Mice in two samples (12, 19) to the northwest of the type locality of *minor*, in southern Morelos, are progressively smaller than material from near the type locality, and average the smallest of the species with the possible exception of specimens from the vicinity of Ebano, San Luis Potosí. There is a name available, *exiguus* (Elliot, 1903), for the material from southern Morelos, but I do not feel that the differences between it and typical *torridus* are sufficient to warrant recognition. Also, the differences are clinal in nature, with the material from southern Morelos grading smoothly into samples to the southeast and into samples to the north; in neither of these directions have I been able to detect a sharp break in the trend of variation.

Hooper and Handley (1948:13-14) hinted at the possibility that the holotype of *Liomys irroratus minor* is in reality a specimen of *Liomys pictus*. This brings up the possibility that the name *minor* could be the proper name for the race that is herein recognized as *Liomys pictus plantinarensis*. In a discriminant function analysis that will be discussed more fully in the section on specific relationships, discriminant multipliers were generated for three external and nine cranial measurements (zygomatic breadth excluded) using a reference sample of *Liomys pictus* from Michoacán and northwestern Guerrero and a reference sample of *Liomys irroratus* from south of the Río Balsas in Guerrero (Fig. 48). The discriminant scores for the *pictus* reference sample ranged from 40.236 to 43.263 and those for the *irroratus* reference sample ranged from 44.633 to 49.135. When the measurements of the holotype of *minor* were multiplied by the discriminant multipliers a score of 46.051 was obtained. This value is clearly in the range for *Liomys irroratus* and I believe the holotype of *minor* is a representative of this species.

The length of ear of six adult males and seven adult females of *Liomys irroratus torridus* from western Puebla averaged, respectively, 15.7 (14.0-17.0) and 14.9 (13.0-16.0); weights of these same individuals averaged 44.8 (39.0-51.5) and 37.3 (32.0-43.0).

Specimens examined (710).—GUERRERO: ½ mi. W Acahuizotla, 3000 ft., 1 (UMMZ); 16 km. N Agua del Obispo, 4400 ft., 1 (KU); 9 km. N Agua del Obispo, 3850 ft., 5 (KU); 5½ km. N Agua del Obispo, 3400 ft., 17 (KU); 5¼ km. N Agua del Obispo, 3350 ft., 3 (KU); 5 km. N Agua del Obispo, 3400 ft., 2 (KU); 2½ mi. S Almolonga, 5600 ft., 8 (6 TCWC, 2 UNAM); Ayotzinapa, 1 (USNM); 7 km. SW Cacahuamilpa, 1 (UNAM); Cahuilotal, Sacacoyuca, 960 m., 14 (5 KU, 9 UNAM); Cerro Chamilpa, 12 km. ESE Chilpancingo, 1400 m., 6 (4 KU, 2 UNAM); 1 km. NW Chapa, 1470 m., 11 (7 KU, 4 UNAM); Chapa, 1470 m., 11 (5 KU, 6 UNAM); 4 mi. W Chilpancingo, 5800 ft., 3 (TCWC); Chilpancingo, 103 (24 FMNH, 3 MCZ, 7 MVZ, 57 UMMZ, 6 UNAM, 6 USNM); 15 km. S Chilpancingo, 4300 ft., 4 (TCWC); Cocula, 1 (ENCB); 15 km. NNE Iguala, 1025 m., 2 (UNAM); Iguala, 730 m., 8 (UMMZ); 3.2 km. SSE Iguala, 970 m., 5 (2 KU, 3 UNAM); La Cofradia, Teloloapan, 2 (KU); Laguna Honda, 1½ km. SSW Yerbabuena, 1840 m., 1 (KU); 2 km. ENE Los Sabinos, 1400 m., 3 (2 KU, 1 UNAM); Mazatlán, 1 (MVZ); Ojo de Agua de Chapa, 5 km. SE Teloloapan, 1520 m., 12 (UNAM); Sacacoyuca, 1 (KU); Sochi, 1 (USNM); 17 km. S Taxco, 4000 ft., 6 (TCWC); 4 3/10 mi. N Teloloapan, 3 (UNAM); Teloloapan, 13 (UMMZ); Texcalzintla, 6 km. NNW Teloloapan, 18 (10 KU, 8 UNAM); 1 km. SSE Texcalzintla, 1600 m., 8 (3 KU, 5 UNAM); 2 mi. N Tixtla, 4400 ft., 4 (TCWC); 3 km. E Tixtla, 3 (ENCB); Tlalixtaquilla, 2 (USNM); Tlapa, 5 (USNM); 2 km. W Tomatal, 970 m., 1 (KU); 2 mi. W Xochipala, 4400 ft., 16 (MSU); Yerbabuena, 1850 m., 1 (KU); 1½ mi. SE Zumpango, 4000 ft., 1 (TCWC).

MORELOS: 3 mi. N Alpuyeca, 4000 ft., 4 (TCWC); 3 km. N Alpuyeca, 1100 m., 1 (ENCB); Alpuyeca, 4000 ft., 5 (TCWC); 1 mi. E Alpuyeca, 3500 ft., 1 (TCWC); 12 km. NW Axochiapan, 3500 ft., 2 (TCWC); 20 km. NE Cuautla, 6500 ft., 1 (TCWC); 20 km. NE Cuernavaca, 2100 m., 2 (ENCB); Cuernavaca, 8 (USNM); near Cuernavaca, 2 (CAS); 12 mi. S Cuernavaca, 4500 ft., 2 (MVZ); 150 m. SE Huajintlán, 920 m., 3 (UNAM); ¼ mi. SE Huajintlán, 3000 ft., 1 (TCWC); 1½ mi. SE Huitzilac, 8000 ft., 8 (TCWC); 2 km. SW Jonacatepec, 4500 ft., 1 (TCWC); Las Animas, Temixco, 1340 m., 1 (UNAM); 2 mi. SW

Michapa, 5000 ft., 1 (TCWC); Puente de Ixtla, 6 (2 FMNH, 4 USNM); ½ mi. W Tehuixtla, 960 m., 1 (UNAM); Temilpa, 8 (4 TCWC, 4 UNAM); 5 mi. W Tepoztlán, 6000 ft., 3 (TCWC); Tepoztlán, 6000 ft., 2 (UMMZ); 2 mi. SW Tepoztlán, 7000 ft., 6 (TCWC); Tequesquitengo, 900 m., 4 (UMMZ); Tetecala, 4 (FMNH); 6 mi. W Yautepec, 4500 ft., 14 (TCWC); Yautepec, 21 (USNM).

OAXACA: 3 km. NNE Cuicatlán, 600 m., 1 (KU); 1 km. N Cuicatlán, 560 m., 3 (UNAM); 1 km. NNW Cuicatlán, 560 m., 6 (2 KU, 4 UNAM); Cuicatlán, 600 m., 45 (2 KU, 5 UMMZ, 1 UNAM, 37 USNM); 1 km. S Ciucatlán, 590 m., 2 (1 KU, 1 UNAM); Huajuapan de León, 1600 m., 16 (12 UMMZ, 4 USNM); Teotitlán, 950 m., 71 (11 FMNH, 60 UMMZ); Tlapancingo, 1 (USNM).

PUEBLA: 1 mi. NNE Acatlán, 3900 ft., 4 (KU); Acatlán, 2 (USNM); Atlixco, 5 (USNM); 3 mi. S Chila, 5900 ft., 1 (MSU); 5 mi. NNW Izúcar de Matamoros, 5 (KU); 3 mi. N Izúcar de Matamoros, 4250 ft., 4 (KU); 3 mi. W, 1 mi. S Izúcar de Matamoros, 9 (KU); 6½ mi. SW Izúcar de Matamoros, 7 (KU); 8 mi. SE Izúcar de Matamoros, 3 (CAS); Matamoros, 2100 m., 2 (1 UMMZ, 1 UNAM); Piaxtla, 19 (USNM); 7 mi. S, 3 mi. E Puebla, 6850 ft., 8 (KU); San Martín, 4 (USNM); 20 km. N Tehuacán, 2110 m., 1 (UNAM); Techuacán, 31 (30 UMNZ, 1 USNM); 1½ mi. W Tehuitzingo, 3570 ft., 5 (KU); Tepanco, 17 (UMMZ); 1 mi. SSW Tilpa, 3700 ft., 9 KU); 4½ km. E Totimehuacán, 2150 m., 1 (ENCB); 6 km. E Totimehuacán, 2150 m., 3 (ENCB).

VERACRUZ: 4 km. W Acultzingo, 7500 ft., 1 (KU); Acultzingo, 2 (UMMZ); 4 mi. SW Acultzingo, 7000 ft., 1 (KU).

Additional records.—MORELOS: 10 mi. N Cuautla (Davis and Russell, 1954:73). PUEBLA: Amolac (Goldman, 1911:55).

Marginal records.—PUEBLA: San Martín; 6 km. E Totimehuacán, 2150 m. VERACRUZ: Acultzingo. OAXACA: Teotitlán, 950 m.; 3 km. NNE Cuicatlán, 600 m.; *1 km. S Cuicatlán, 590 m.*; Huajuapan de León, 1600 m.; Tlapancingo. GUERRERO: Tlalixtaquilla; 5 km. N Agua del Obispo; 4 mi. W Chilpancingo, 5800 ft.; 2 mi. W Xochipala, 4400 ft.; *Texcalzintla, 6 km. NNW Teloloapan; Laguna Honda, 1 1/2 km. SSW Yerbabuena, 1840 m.;* Yerbabuena, 1850 m.; 7 km. SW Cacahuamilpa. MORELOS: *2 mi. SW Michapa, 5000 ft.;* Tetecala; *Cuernavaca;* 1½ mi. SE Huitzilac, 8000 ft.; 20 km. NE Cuernavaca, 2100 m.; 20 km. NE Cuautla.

Liomys pictus

Painted Spiny Pocket Mouse

Liomys pictus occurs along the west coast of México from a place 23 mi. S and 5 mi. E Nogales, Sonora, southward through Sonora, Sinaloa, Durango, Nayarit, Jalisco, Colima, Michoacán, Guerrero, and Oaxaca. In this area the species is generally restricted to the coastal lowlands and adjacent slopes of the Sierra Madre Occidental and Sierra Madre del Sur; however, in Jalisco, Michoacán, and Guerrero one subspecies is restricted to interior valleys and large river systems. Along the Pacific coast, *L. pictus* occurs as far south as the vicinity of Tonalá, Chiapas, but specimens are known from throughout the central valley of Chiapas and from one locality (Nentón) in Guatemala. The species also is known from several localities in the Isthmus of Tehuantepec and from along the east coast from southern Veracruz northward to San Carlos in central Veracruz.

Diagnosis

External and cranial measurements medium to small for the genus, although some populations (*annectens*) are relatively large in size; cranium relatively narrow in comparison with length; protoloph of upper premolar generally appearing to be composed of a single cusp; three cusps of metaloph connected by loph so as not to form discrete cones; hypocone largest cusp on metaloph; entostyle always connected to hypocone by loph; re-entrant angle on labial margin of lower premolar not reaching median valley; baculum long and with a small rounded base, distal end of shaft with ventral keel that is laterally compressed and the shaft dorsoventrally compressed posterior to terminal keel; glans penis short when compared with baculum, tip of glans long; glans but slightly sculptured; urethral lappets trilobed; 2N = 48; FN = 66; head of spermatozoon long and with pointed apex; distinct neck between head and midpiece of spermatozoon; wings of pterygoids narrow; parasitized by the anopluran, *Fahrenholzia microcephala*; six plantar tubercles on most specimens, although some individuals of *L. p. plantinarensis* have only five; upper parts reddish brown; lateral stripe generally ochraceous, but may be rather pale; underparts white; hairs on back not curled upward so as to be conspicuous above spines.

Comparisons

From *Liomys spectabilis*, sympatric populations of *Liomys pictus* (subspecies *plantinarensis*) can be distinguished easily by much smaller size. There is no overlap in measurements of adults of the two taxa for total length, length of hind foot, greatest length of skull, interorbital constriction, mastoid breadth, length of nasals, and length of rostrum, and specimens of *plantinarensis* average significantly smaller in all other measurements analyzed. Populations of *L. pictus* (subspecies *pictus*) from coastal areas of western Jalisco are again distinguished from *L. spectabilis* by smaller size, although the difference is not as striking as in the case of *plantinarensis*. Only in greatest length of skull and length of rostrum is there no overlap in measurements of the two taxa, although *pictus* averages smaller in all measurements except for those of the interparietal bone. A useful character in separating these two taxa externally is length of hind foot, which is rarely more than 30 in *pictus* and rarely less than 30 in *spectabilis*. The only subspecies of *L. pictus* that approaches *L. spectabilis* in size is *annectens* from the mountains of Guerrero and Oaxaca. From this race, *spectabilis* can be distinguished by its slightly larger overall size and proportionately shallower cranium. The morphology of the baculum of *L. pictus* and *L. spectabilis* is essentially identical but the ventral keel on the distal end of the shaft is shorter in 11 specimens of *pictus* (0.85-1.25) than in two specimens of *spectabilis* (both 1.30). Both species have 48 chromosomes, but *pictus* has one more pair of metacentrics, giving it a fundamental number of 66 as opposed to 64 for *spectabilis*. The morphology of the head and neck regions of the spermatozoon of *pictus* and *spectabilis* is similar, but the head of the sperm of *pictus* is significantly shorter and narrower than that of *spectabilis*. The dorsal coloration of the two species is similar, but specimens of *plantinarensis* are paler than *spectabilis*, whereas specimens of *annectens* are darker.

Liomys pictus can be distinguished from *Liomys salvini*, especially in the zone of sympatry, by its much larger overall size (particularly total length, length of tail, interorbital constriction, length of nasals, and interparietal length). The entostyle on the upper premolar is less distinctly separated from the remaining cusps in *pictus* than in *salvini* and re-entrant angle on the labial margin of the lower premolar reaches the median valley in specimens of *salvini* but not *pictus*. The baculum of *pictus* has a distal ventral keel that is laterally compressed, which is lacking in *salvini*; both species have a section of the shaft of the baculum that is dorsoventrally flattened. The glans penis of *pictus* can be distinguished from that of *salvini* by its shorter length in comparison with the length of the baculum, longer tip, and less external sculpturing. The urethral lappets of *pictus* are trilobed, whereas those of *salvini* are bilobed. The karyotype of *L. pictus* reveals 48 chromosomes with a fundamental number of 66, whereas the karyotype of *L. salvini* has 56 chromosomes with a fundamental number of 86. The spermatozoon of *pictus* has a long head with a pointed apex as compared with that of *salvini*, which has a short head with a blunt, broadly rounded apex. Specimens of *L. pictus* are parasitized by the anopluran *Fahrenholzia microcephala*, whereas *L. salvini* is parasitized by *Fahrenholzia fairchildi*; the upper parts of *pictus* are reddish brown with an ochraceous lateral stripe, but *salvini* has chocolate brown or paler upper parts and lacks a lateral stripe; the hairs on the back of specimens of *salvini* are curled upward and are visible above the spines, but this is not true of specimens of *pictus*.

Liomys pictus can be distinguished from *Liomys adspersus* by its smaller overall size except for interorbital constriction and width of the interparietal bone, which are usually actually broader in *pictus* and always proportionally so. The entostyle on the upper premolar is less distinctly separated from the remaining cusps in *pictus* than in *adspersus*, and re-entrant angle on the labial margin of the lower premolar reaches the median valley in specimens of *adspersus* but not *pictus*. The baculum, glans penis, and urethral lappets of *pictus* differ from those of *adspersus* in the same ways as from those of *salvini*. *L. pictus* has 48 chromosomes with a fundamental number of 66, whereas *L. adspersus* has 56 chromosomes with a probable fundamental number of 84. The spermatozoon of *pictus* has a long head with a pointed apex, whereas the head of the spermatozoon of *adspersus* is short with a blunt, broadly rounded apex. Specimens of *pictus* are parasitized by *Fahrenholzia microcephala*, whereas *L. adspersus* is parasitized by *Fahrenholzia fairchildi*; the upper parts of *pictus* are reddish brown with an ochraceous lateral stripe, but *adspersus* has chocolate brown or paler upper parts with no lateral stripe; the hairs on the back of specimens of *adspersus* are curled upward and are visible above the spines, however, this is not true of specimens of *pictus*.

For comparisons of *Liomys pictus* with *Liomys irroratus*, see the account of that species.

Ecology

The habitats occupied by *Liomys pictus* are extremely variable, ranging from Sonoran desert in northwestern México to arid lowland tropics along both west and east coasts and to cloud forest in the mountains of Guerrero and Oaxaca. The known altitudinal range of the species is from sea level to approximately 7300 feet at Omilteme, Guerrero, and Río Molino, Oaxaca. *Liomys pictus* appears to prefer moist habitats along rivers and streams in otherwise relatively xeric inland situations; this is especially evident in areas of sympatry with *Liomys irroratus*. In all such cases except one of which I have knowledge, *pictus* occurs in the moist lowlands and *irroratus* in the drier uplands. The one exception is near La Cima, Oaxaca, in a cloud forest situation, where the two species have been taken in what appears to be the same habitat. The other places where the two have been taken together in Jalisco and Guerrero are areas of close contact between upland and lowland habitats. Along the arid coasts, the species appears to be more or less generally distributed, although based upon my own experience and information I have gleaned from field notes of collectors, the painted spiny pocket mouse is, even here, more abundant in moist situations along rivers and streams than in the dry thorn forest. No comprehensive study has been undertaken on the ecology of this mouse but additional natural history information may be obtained from several other sources, notable among which are Baker and Greer (1962:104), Burt (1938:43), Hall and Dalquest (1963:283-284), Hooper (1955:9), and Wagner (1961:207). Briefly discussed below are 11 localities from which *Liomys pictus* has been obtained. These localities are from throughout the range of the species and give some idea of the diverse types of situations under which it lives.

Alamos, 54 km. E Navajoa, 1000 ft., Sonora [approximately 4 miles by road northwest of Alamos according to field notes of collector].—P. L. Clifton, field representative from The University of Kansas, collected at this site between 22 and 29 January 1962. The vegetation in the area was subtropical thorn forest; most trees were about 10 feet tall, and so close together that it was difficult to walk between them. At least two species of tall cactus also grew there. Clifton noted that the vegetation near Alamos closely resembled that found in the vicinity of San Blas and El Fuerte in northern Sinaloa. Traps were placed under bushes and cacti along the edge of a weedy cornfield. Forty-five small rodents including four *Liomys pictus* were taken in 131 traps set the first night. The second night another 100 traps were set in this same area and yielded 19 small rodents of which three were *Liomys pictus*. On this same night Clifton set 55 mouse traps among the rocks on a low tree-clad hill; these traps did not yield *Liomys* nor did 82 traps set in the same type of habitat on the third night. On the night of 25 January traps again were placed in the same general area as on the first night and from 120 museum special traps 40 small rodents (of which three were *Liomys pictus*) were removed. Burt (1938:43) noted that in southern Sonora *Liomys* was abundant around cultivated fields and their food "consisted chiefly of seeds of cultivated beans and wheat." Small rodents trapped along with *Liomys* at Alamos included *Perognathus artus*, *P. goldmani*, *P. pernix*, *Dipodomys merriami*, *Reithrodontomys fulvescens*, *Peromyscus eremicus*, *P. merriami*, *Onychomys torridus*, *Sigmodon arizonae*, *Neotoma albigula*, and *N. phenax*.

1/2 mi. S Concepción, 250 ft., Sinaloa.—This locality, which is along the Río de las Cañas, was visited by J. K. Jones, Jr., and R. R. Patterson between 26 and 28 February 1961 and by E. C. Birney, L. C. Watkins, and me between 14 and 16 August 1969. The general vegetation in the area was arid thorn forest. Most of the trees were about 10 feet tall and grew in dense stands with open grassy areas between the stands. Above the bed of the river some of the area is cultivated but along the sloping banks of the river was a relatively dense stand of thorny scrub. Traps were placed along the sandy sloping bank in an area of thorn brush and grass adjacent to a cornfield. From this area only *Perognathus pernix* and *Liomys pictus* were trapped, with the Sinaloan pocket mouse being the more abundant of the two species. In the general vicinity, specimens of *Neotoma alleni* and *Sigmodon arizonae* were also obtained.

11 mi. SW Autlán, 2000 ft., Jalisco.—This locality is on the Pacific slope of the first major range of mountains inland from the coast. When I visited this location on 1 July 1966, and 11 August 1969, during the rainy season, the area was extremely wet; fog hung along the slopes, at least in the morning, and rain occurred at nearly any time of the day. Clifton worked here in the dry season (4 March 1966) and noted "the tropical deciduous forest is still green on the north slopes and in the arroyos." Traps were set in a deep arroyo that had a small stream running through it. The arroyo was never more than 50 feet wide and deciduous trees (70 to 100 feet tall) and brush grew in the bottom almost to the edge of the stream. Traps were placed at holes in the bases of trees, along the wall of the arroyo where overhanging rock and brush formed a protective cover, and under the many boulders near the stream. In addition to *Liomys pictus*, specimens of *Peromyscus banderanus* and *Oryzomys palustris* were obtained.

5 km. NNW Barro de Navidad, Jalisco.—M. R. Lee collected mammals at this locality from 24 March to 2 April 1961. Lee made his camp at the base of a cliff in a coco-oil palm grove; vegetation above the cliff was low thorn forest. One hundred and fifty snap traps were set among boulders at the base of the cliff where little or no vegetation was actually growing among the rocks. These traps yielded seven *Peromyscus banderanus*, one *Liomys pictus*, and three *Neotoma alleni*. The following night 150 traps were set on the hill above the cliff where the vegetation consisted of sparse grass, several kinds of cactus, and low shrubby trees and bushes; nearly all of the trees were without leaves. Only two *Peromyscus banderanus* and one *Liomys pictus* were obtained in these traps. The remaining time at this locality Lee trapped around the edge of a marsh where cattails and long grass were the major vegetation. No spiny pocket mice were captured near the marsh, although many small rodents including *Oryzomys palustris*, *O. melanotis*, *Peromyscus banderanus*, *P. perfulvus*, and *Sigmodon mascotensis* were obtained there.

2 7/10 mi. WNW Zapotiltic, 5000 ft., Jalisco.—This area, which is near Ciudad Guzmán, is heavily agriculturized. Most of the land in the valleys is cultivated (mainly with corn) and the hills are grazed; scattered trees that grew on the hills were mostly deciduous types but conifers were found on some of the upper slopes. In the areas between trees, clumps of brush are obtained, especially in slight depressions. Clifton, who trapped at this place on 5 and 6

March 1964, placed his traps in the weeds along a rock fence around an old cornfield. Only specimens of *Liomys pictus* and *Liomys irroratus* were obtained with *Liomys pictus* being much commoner than *irroratus*. At a locality only a short distance away—3½ mi. WNW Zapoltitic, 5100 feet—in essentially the same type of habitat, *Liomys irroratus* was the much commoner species.

5 km. N Agua del Obispo, 3250 ft., Guerrero.—The town of Agua del Obispo is approximately 35 km. S Chilpancingo on the road to Acapulco and is situated on the Pacific slope of the Sierra Madre del Sur. The vegetation in the area is characterized by pine-oak forest on the more arid slopes and dense tropical deciduous trees in the valleys. On 11 June 1964, Clifton placed 50 museum special traps baited with walnuts and oatmeal among the trees in one of the wet valleys. From these traps he removed 14 *Liomys pictus*, one *Megasorex gigas*, and one *Oryzomys palustris*. Clifton revisited this locality on the night of 13 June 1964, when he obtained five *Liomys pictus* and one *Megasorex gigas* from 100 traps that were baited with tuna fish and placed under rocks and rotten logs. At a nearby locality—5¼ km. N Agua del Obispo, 3350 feet—Clifton obtained both *Liomys pictus* and *Liomys irroratus*. Specimens of *Liomys pictus* all were caught in a dense stand of deciduous trees along a creek, whereas *L. irroratus* was taken in a more open and drier situation where low brush predominated.

10 mi. S Juchatengo, 5350 ft., Oaxaca.—This locality is situated in dense cloud forest along the Pacific Slope of the Sierra Madre del Sur. On the night of 7 July 1964, Clifton placed 28 traps in 10-foot-high brush around the edge of an old cornfield that was situated in a clearing in the forest. From these traps he removed specimens as follows: *Liomys pictus*, 4; *Peromyscus megalops*, 5; *P. evides*, 3; *Neotoma mexicana*, 1. On the night of 8 July 43 traps were placed around the cornfield and 30 traps were set under rocks and logs near a stream in the cloud forest. These traps yielded the following specimens: *Liomys pictus*, 6; *Peromyscus megalops*, 6; *Oryzomys palustris*, 1; *Reithrodontomys sumichrasti*, 1.

Puerto Angel, Oaxaca.—R. W. Dickerman worked in the area around Puerto Angel from 3 to 9 September 1954 collecting vertebrates for the Museum of Natural History. He described the general area as arid lowland tropics but in the stream valleys the vegetation was nearly as lush as along the streams higher in coastal ranges. On 4 September Dickerman set traps along a hill facing the bay in low xeric vegetation and along a dry stream bed where the vegetation was slightly more lush. Obtained in these traps were three *Liomys pictus*, one *Peromyscus mexicanus*, and two species of crabs. On the evening of 6 September traps were placed among rocks and at the bases of trees along a large intermittent stream near the town. The only species obtained was *Liomys pictus* (seven specimens). Trapping the following night in the same habitat yielded three *Liomys pictus* and one *Peromyscus mexicanus*.

Finca San Salvador, 15 km. SE San Clemente, 1000 m., Chiapas.—From 3 to 7 August 1965, a field party under the direction of James D. Smith collected mammals and their ectoparasites at this location in the valley of the Río San Clemente. In the valley along the river were planted corn, bananas, and sugar cane and tall grass grew along the banks of the river. On the hills above the valley grew a pine-oak forest with pine becoming predominant on the upper slopes. Smith described this forest as having the appearance of a "parkland." Some traplines were set in the grass and cane along the river, whereas others were placed from the river up into the forest. Specimens of *Liomys pictus* were trapped both in the valley and on the upper slopes; however, they appeared, as did other rodents, to be more abundant in the valley. Other species of small rodents collected at this locality in addition to spiny pocket mice included *Oryzomys palustris*, *O. fulvescens*, *Peromyscus boylii*, *P. mexicanus*, *Baiomys musculus*, and *Sigmodon hispidus*.

3 km. E San Andrés Tuxtla, 1000 ft., Veracruz.—At this locality a large series of *Liomys pictus* was obtained by W. W. Dalquest between 7 and 18 January 1948. The mice were taken in a variety of places, including at the edge of dense tropical forest and near a small lake. Although a large number of traps were placed in the forest, no painted spiny pocket mice were taken there. Most of the specimens were trapped in brush and tall grass at the

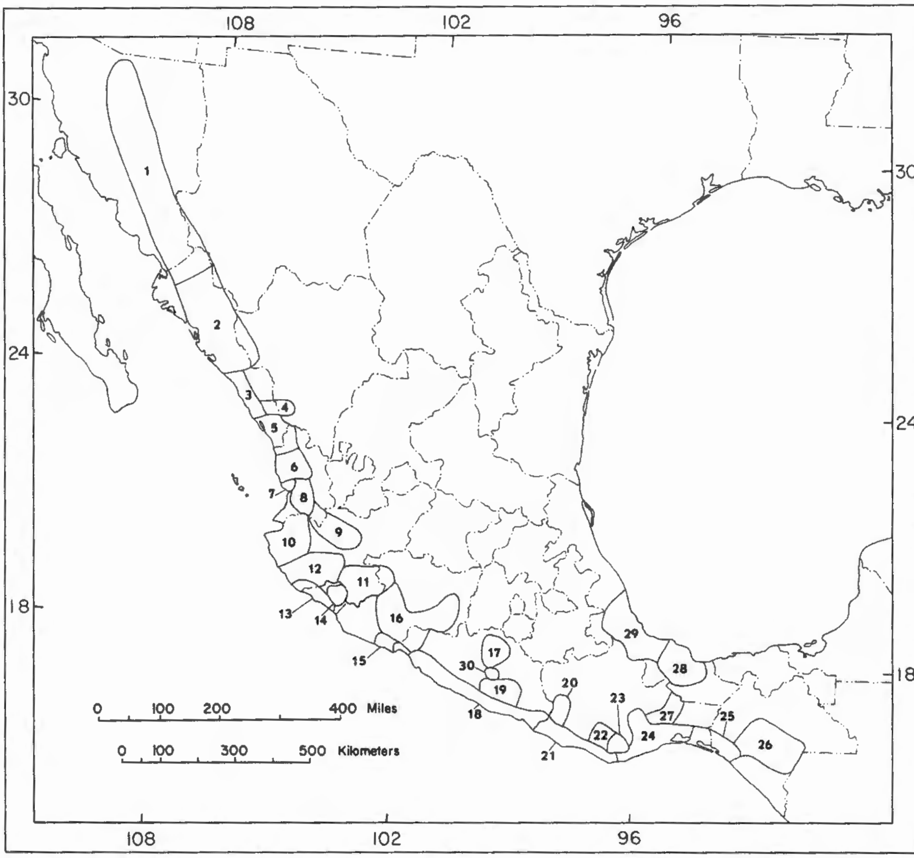


FIG. 19.—Approximate geographic areas included in the 30 samples of *Liomys pictus*. See text for localities included in each sample.

edge of fields and pastures. Other small rodents recorded from this locality were *Oryzomys palustris*, *O. melanotis*, *O. fulvescens*, *Tylomys nudicaudus*, *Peromyscus mexicanus*, *Sigmodon hispidus*, and *Mus musculus*.

Río Blanco, 20 km. WNW Piedras Negras, 400 ft., Veracruz.—This locality is situated on the coastal plains of Veracruz where the vegetation can be described as typical of the arid tropics. There were extensive grasslands broken by thickets of dense thorny shrubs, principally bullhorn acacia. Along the arroyos and the Río Blanco was extremely dense deciduous forest. W. W. Dalquest trapped this area from 11 to 29 May 1946. Although trapping in the bunchgrass and acacia did yield a few small rodents, Dalquest found the areas of dense vegetation in the arroyos and along the river much more productive. Only one *Liomys pictus* was taken in the extensive area of bunchgrass; it was taken in a trap set on sandy soil between the bunches of grass and at least 100 yards from the nearest patch of brush and even further from the nearest forested area. Four nights of trapping in the grass and acacia shrub yielded only four specimens of *Liomys pictus*, whereas two nights of trapping in the forest along an arroyo yielded six specimens. The ground in the forest was dry and relatively free of underbrush; however, there was considerable dry grass and a cover of dry leaves. Other small rodents taken at this locality were *Reithrodontomys fulvescens*, *Peromyscus mexicanus*, *Baiomys musculus*, and *Sigmodon hispidus*.

Geographic Variation

Univariate Analysis

Nearly all adult specimens from throughout the geographic range of *Liomys pictus* were grouped into 28 samples for males and 29 samples for females as follows (Fig. 19): *sample 1*—Sonora (Alamos, Camoa, El Novillo, Guirocoba, Matape, Nacori, Nogales, Río Alamos, Río Cuchahaqui), Chihuahua (labeled with reference to Choix, Sinaloa), and Sinaloa (Choix, El Fuerte); *sample 2*—Sinaloa (Agua Nueva, Cosalá, Culiacán, El Dorado, Guamúchil, Guasave, Pericos, Sinaloa) and Durango (Chacala); *sample 3*—Sinaloa (Camino Real, La Cruz, Mazatlán, San Ignacio, north of Villa Unión); *sample 4*—Sinaloa (Copala, Hacienda San José, Santa Lucía) and Durango (Pueblo Nuevo); *sample 5*—Sinaloa (Concepción, Escuinapa, Isla Palmito de la Virgen, Isla Palmito del Verde, La Concha, Matatán, Plomosas, Rosario, Teacapán) and Nayarit (Acaponeta, Huajicori, Playa Novilleros); *sample 6*—Nayarit (Plantanares, Rosamorada, Tuxpan); *sample 7*—Nayarit (San Blas); *sample 8*—Nayarit (Compostela, Ixtlán del Río, Santa Isabel, Tepic); *sample 9*—Nayarit (Amatlán de Cañas, Ojo de Agua, Rancho Palo Amarillo) and Jalisco (Guadalajara); *sample 10*—Nayarit (Las Varas, San Francisco, Valle de Banderas) and Jalisco (La Cuesta, Milpillas, Puerto Vallarta, San Sebastián); *sample 11*—Jalisco (Atenqueque, Contla, Jilotlán de los Dolores, Pihuamo, Platanar, Tamazula, Zapoltitic) and Michoacan (Los Reyes); *sample 12*—Jalisco (Autlán, Durazno, La Resolana, Limón, Purificación, Tapalpa, Tecomate); *sample 13*—Jalisco (Barro de Navidad, Cihuatlán, Cuitzamala, Melaque, Tenacatita) and Colima (Armería, La Gloria, Paso del Río, Santiago, Tlapeixtes); *sample 14*—Colima (Cerro Chino, Colima, Hda. Magdelena, Las Juntas [5 km. SE Pueblo Juárez], Pueblo Juárez); *sample 15*—Michoacan (Arteaga, La Mira—this sample includes only two adult males); *sample 16*—Michoacan (Apatzingán, La Huacana, La Salada, Tacámbaro, Tumbiscatio, Tzitzio) and Guerrero (El Limón); *sample 17*—Guerrero (Iguala, Los Sabinos, Río Balsas); *sample 18*—Guerrero (Acapulco, Acapulco Bay, near Ometepec, Sihuatanejo Bay, Zihuatanejo); *sample 19*—Guerrero (Acahuizotla, Agua del Obispo, Chilpancingo, Colotlipa); *sample 20*—Oaxaca (km. 123 Tlaxiaco-Putla Road, La Concepción, San Vincente—this sample contains only females); *sample 21*—Oaxaca (Llano Grande, Jamiltepec, Pinotepa, Pinotepa de Don Luis, Puerto Angel); *sample 22*—Oaxaca (Jamaica Junction, Juchatengo, km. 136 Oaxaca-Puerto Escondido Road, km. 183 Oaxaca-Puerto Escondido Road, km. 198 Oaxaca-Puerto Escondido Road, km. 212½ Oaxaca-Puerto Escondido Road, km. 214 Oaxaca-Puerto Escondido Road, Lacháo, Nopala, San Gabriel Mixtepec, Sola de Vega); *sample 23*—Oaxaca (Candelaria, Chacalapa, Pluma, Río Guajolote, Río Molino); *sample—24*—Oaxaca (Aguaje las Animas, Aguaje Tres Cabezas, Escuranos, Guiengola, Juchitán, La Ventosa, Nejapa, Salazar, Salina Cruz, San José Lachiguirí, Santa Cruz Bay, Santa Lucía, Santa María Ecatepec, Tehuantepec); *sample 25*—Oaxaca (Reforma, Santa Efigenia) and Chiapas (Madre Mía, Tonalá); *sample 26*—Chiapas (Cerro Tres Picos, Chiapa de Corzo, Cinco Cerros, Cintalapa, Comitán, La Trinitaria, Ocozocoautla, Ortiz Rubio, San Clemente, San Gregorio, Tuxtla Gutiérrez); *sample 27*—OAXACA (Ixcuintepec, Lagunas, Santo Domingo); *sample 28*—VERACRUZ (Catemaco, Coatzacoalcos, Jimba, Pasa Nueva, San Andrés Tuxtla); *sample 29*—VERACRUZ (Boca del Río, Carrizal, Otatitlán, Piedras Negras, Presidio, Puente Nacional, San Carlos); *sample 30*—GUERRERO (Omilteme—this sample contains only females). Dice grams (Fig. 20) have been prepared for several of the measurements in order to facilitate the demonstration of trends in geographic variation. Standard statistics are given for each sample of *Liomys pictus* in Table 11.

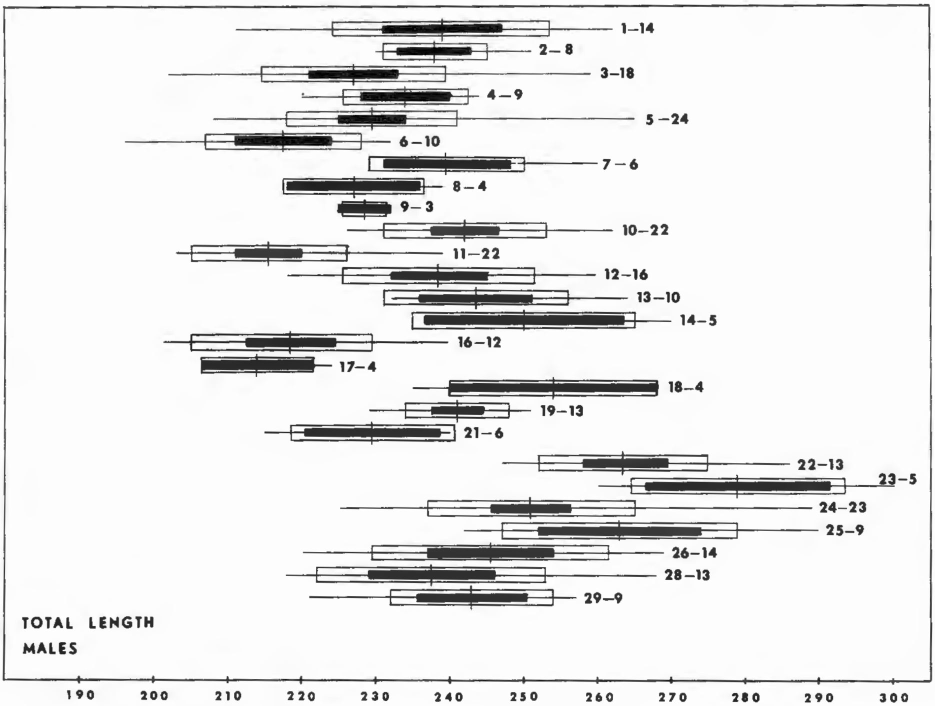
External Measurements

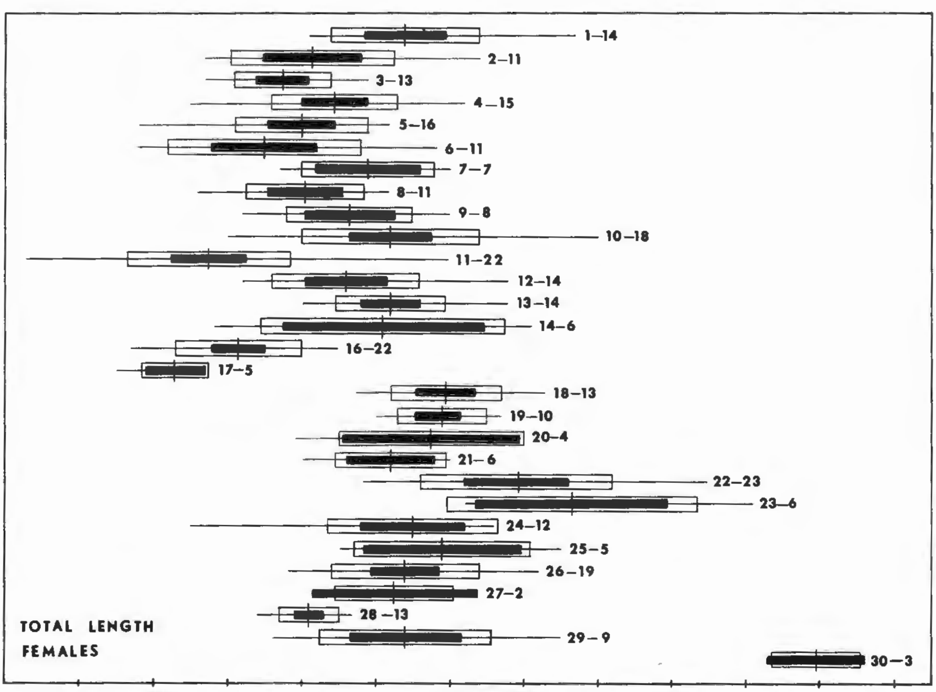
Specimens from Sonora and northern Sinaloa (sample 1) have a mean total length (see Fig. 20 and Table 11) that is intermediate for the species. Progressing southward along the coast of Sinaloa and Nayarit from sample 1 to sample 6, excepting sample 3, there is a relatively smooth cline with means becoming smaller with decreasing latitude. Specimens from the vicinity of Mazatlán, Sinaloa (sample 3), are somewhat smaller than would be expected at that point in the cline. The mean total length of specimens from near San Blas, Nayarit (sample 7), is much greater than that of specimens to the north in the lowlands of Nayarit and more closely resembles that of specimens to the south along the southern coast of Nayarit and on the coast and Pacific slope of the Sierra Madre of Jalisco and Colima (samples 10, 12-14). Specimens from the vicinity of Tepic, Nayarit (sample 8), have a mean total length that is intermediate between that of individuals in the lowlands to the north (6) and those along the coast to the west (7). This is also true of males from southeastern Nayarit and north-central Jalisco (sample 9), although females from the same area are relatively larger and, therefore, approach specimens to the west. Specimens from the interior drainage basins of Jalisco and Michoacán and along the Río Tepalcatepec, Michoacán, and Río Balsas, Guerrero, and their tributaries (samples 11, 16, 17) form a unit characterized by uniformly short total length. They are, except for some individuals from sample 6, the smallest of the species. Specimens from coastal Guerrero (sample 18) and along the Pacific slope of the Sierra Madre del Sur (sample 19) are comparable with those from Colima. Females from the southwestern coast of Oaxaca (sample 21) resemble those from the adjacent part of Guerrero (18), but males from Oaxaca are much shorter in mean total length than their counterparts in Guerrero. Individuals from the high mountains of Guerrero (sample 30, females only) and Oaxaca (samples 22 and 23) have a total length that is (excepting some individuals from sample 25) the longest for the species. Four females from the vicinity of Putla, Oaxaca (sample 20), which is a mountainous area between samples 30, 22, and 23, are smaller than females from adjacent mountainous areas and more nearly resemble specimens from coastal regions of Guerrero and Oaxaca. Specimens from the isthmian region of Oaxaca, Chiapas, and Veracruz (samples 24-29) form a unit that is similar in total length to samples of both sexes from coastal Guerrero (18) and to females from southwestern Oaxaca (21). Females from Los Tuxtlas and adjacent areas of Veracruz (28) have a mean total length that is relatively short as compared with other females from the region of the Isthmus, but this is not shown by males from the same area.

Populations of *Liomys pictus* exhibit essentially the same pattern of variation in length of the tail (Table 11) as they did in total length. However, the smooth cline seen in the variation of mean total length along the northwestern coast (samples 1-6) is not shown by mean tail length, although specimens of both males and females from the southern part of this area do average smaller than those from the northern part. Again, the mean of specimens from sample 7 is large and more nearly comparable to samples to the south (10, 12-14) than to those to the north (4-6). Length of tail of males and females from sample 9 and males from sample 8 average intermediate between those of northern Nayarit (6) and western Nayarit and Jalisco (7, 10). Females from central Nayarit (8) have a mean length of tail that is slightly shorter than that of specimens from northern Nayarit. Specimens from samples 11, 16, and 17 have a mean length of tail that is the shortest of the species. Specimens from the remainder of the samples in western México, the Isthmus in Oaxaca, Chiapas, and Veracruz, with a few exceptions, have a mean length of tail that is essentially the same. Males from sample 21 and females from sample 28 have a shorter measurement than would be expected and this was also shown in the mean total length. Only specimens from sample 23 and the three females from sample 30, of those occurring in the mountains of Oaxaca and Guerrero, have a tail that averages noticeably longer than in specimens from the coastal lowlands; these specimens are the largest of the species.

The variation in length of hind foot (Table 11) of *Liomys pictus* follows closely the pattern of variation shown by the other two external measurements. The pattern of a smooth cline in Sonora, Sinaloa, and northern Nayarit is present again except that individuals from sample 4, which includes specimens from high elevations in Sinaloa and Durango, are the smallest of the group. Specimens from the vicinity of San Blas (sample 7), although larger than specimens from northern Nayarit, average smaller than those from samples 10 and 12 to 14 and more closely resemble specimens from samples 8 and 9. These three samples form a group intermediate in size between the smaller specimens to the north and the larger to the south. The specimens from interior Jalisco, Michoacán, and Guerrero (samples 11, 16, 17) have, on the average, small hind feet, with those from sample 17 being the smallest of the species. The specimens from the mountains of Oaxaca (22, 23) and Guerrero (30), excepting sample 20, average more than 30 in length of the hind foot and are the largest of the species. The remaining samples (18-21, 24-29) include specimens with hind feet that average an intermediate size for the species and agree closely with specimens from western Jalisco and Colima. The males from sample 25 are larger than those from nearby samples as they were in total length, and females from sample 28 are smaller than those from surrounding samples as they were in total length.

FIG. 20.—Dice grams for seven selected measurements of males and females of *Liomys pictus*. See Fig. 9 for method used in constructing these grams. See Fig. 19 and text for key to samples. →


1–14
2–8
3–18
4–9
5–24
6–10
7–6
8–4
9–3
10–22
11–22
12–16
13–10
14–5
16–12
17–4
18–4
19–13
21–6
22–13
23–5
24–23
25–9
26–14
28–13
29–9
TOTAL LENGTH
MALES
190 200 210 220 230 240 250 260 270 280 290 300


1–14
2–11
3–13
4–15
5–16
6–11
7–7
8–11
9–8
10–18
11–22
12–14
13–14
14–6
16–22
17–5
18–13
19–10
20–4
21–6
22–23
23–6
24–12
25–5
26–19
27–2
28–13
29–9
30–3
TOTAL LENGTH
FEMALES
190 200 210 220 230 240 250 260 270 280 290 300

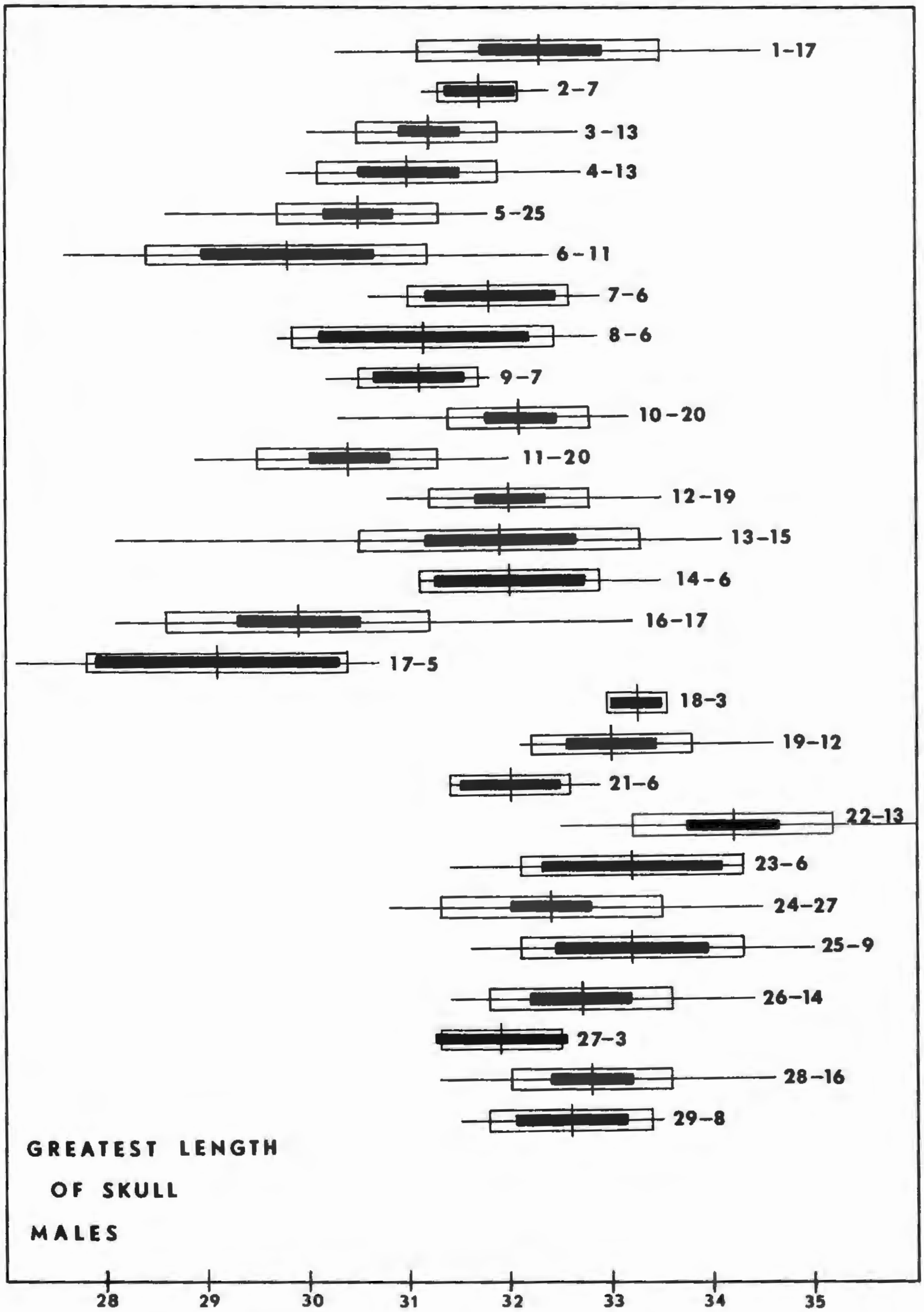
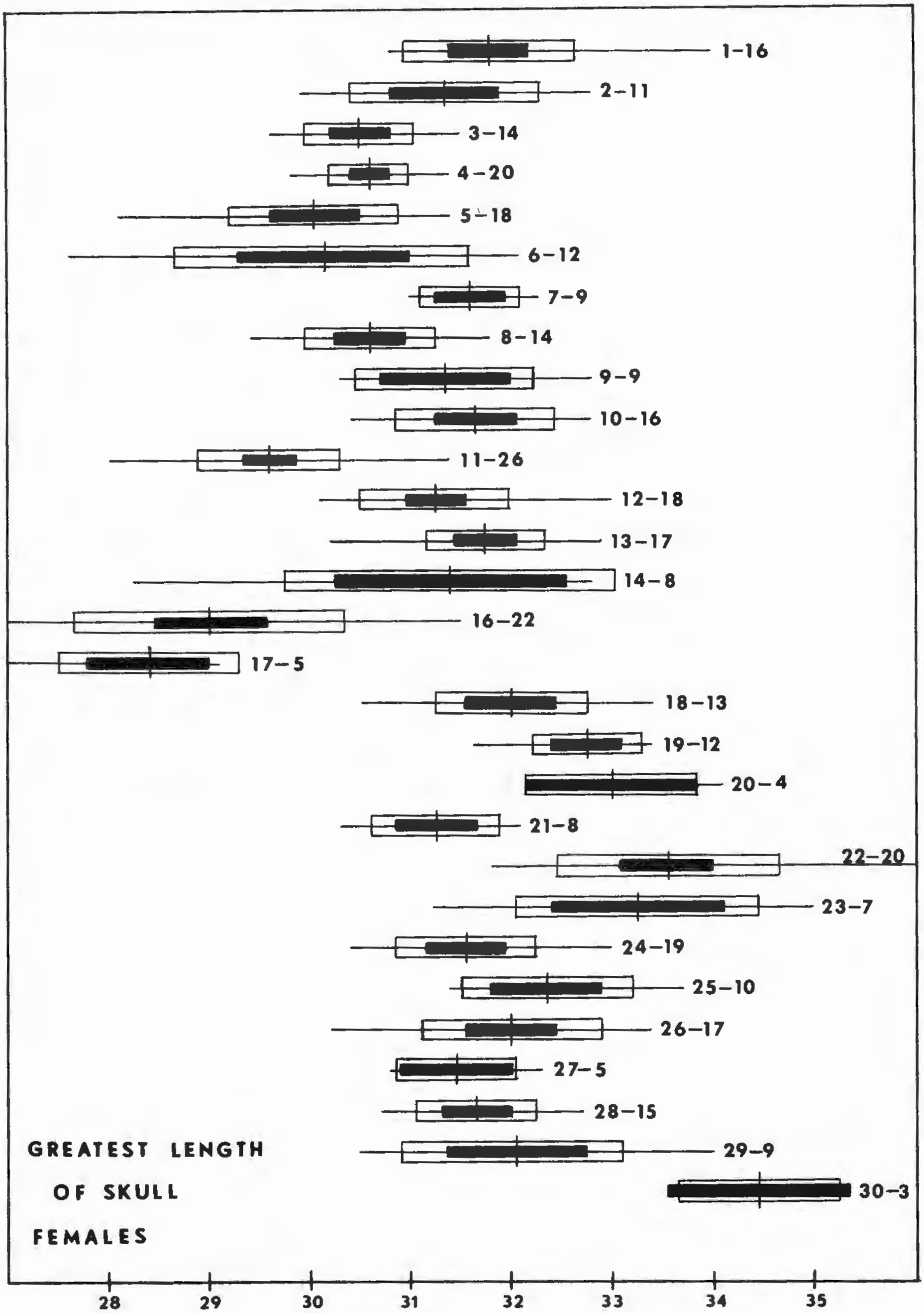


FIG. 20.—Continued.



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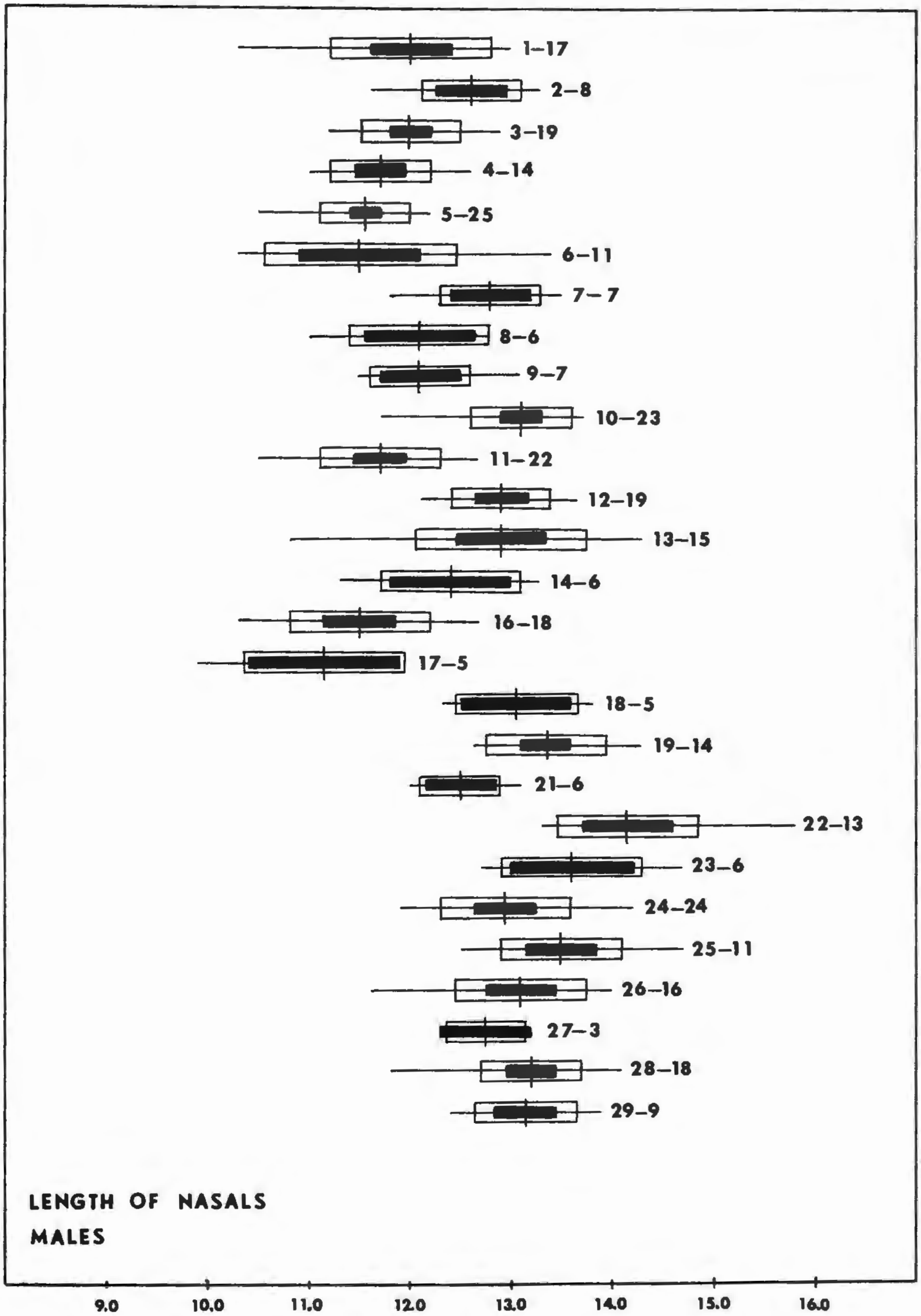

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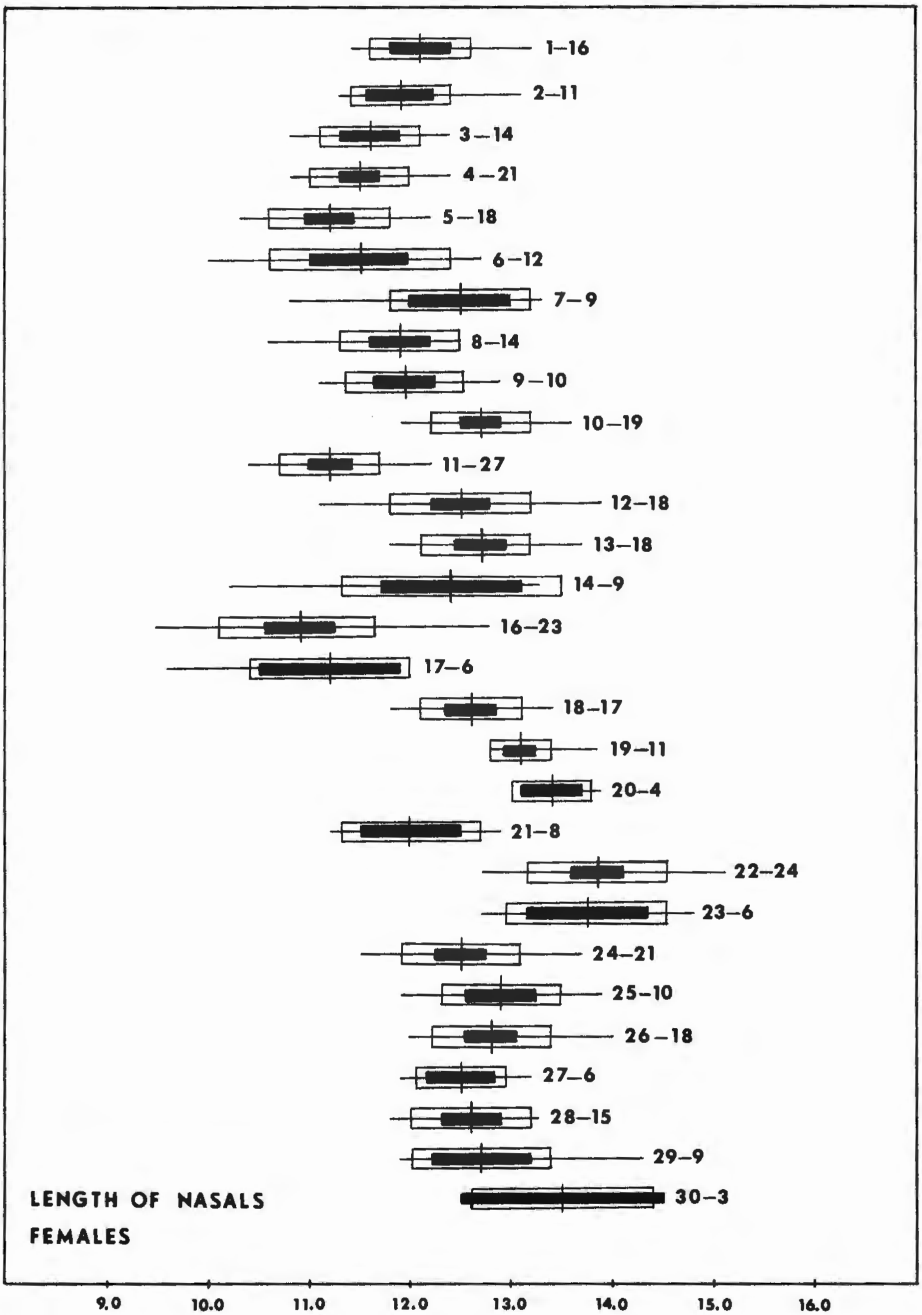

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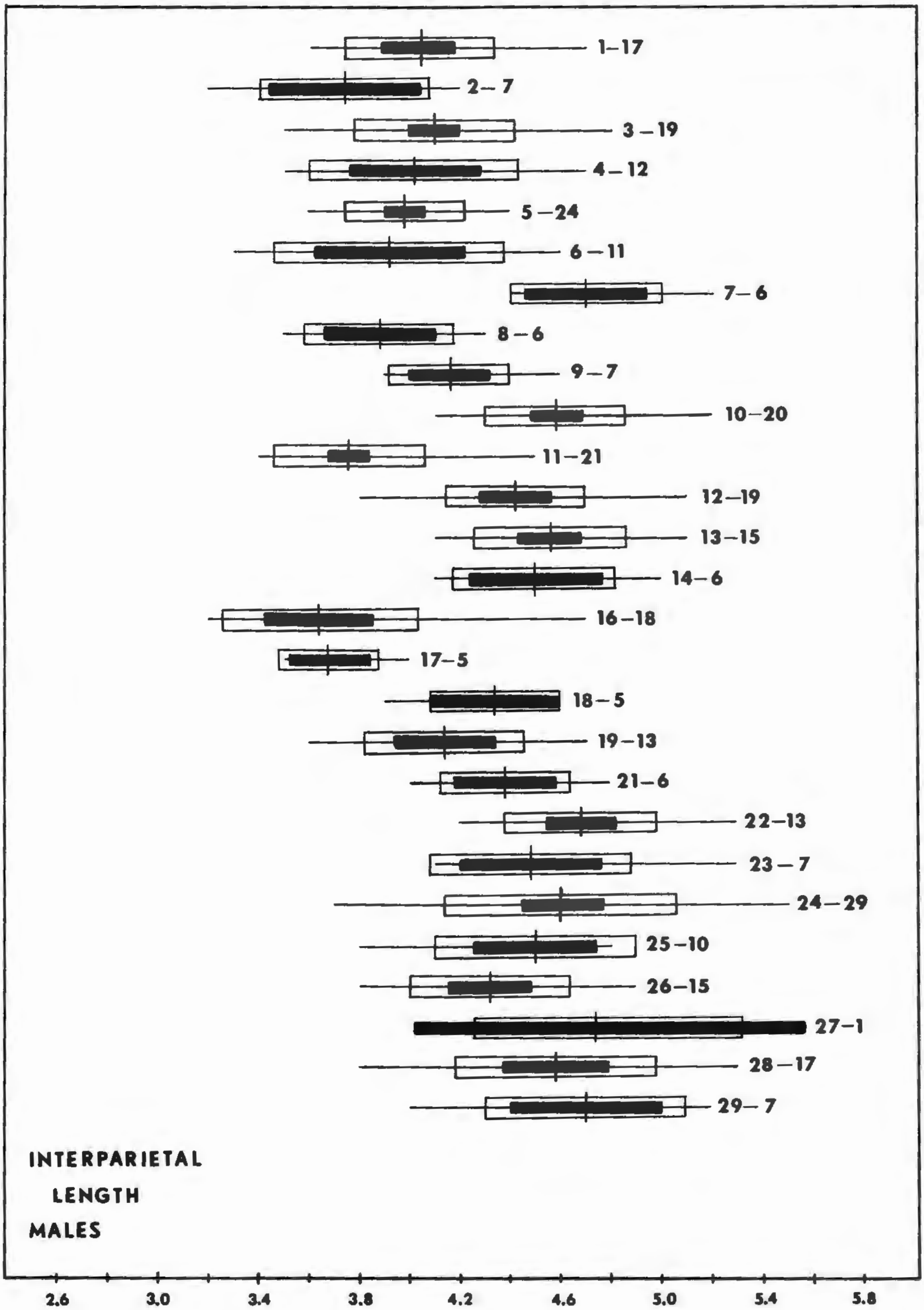

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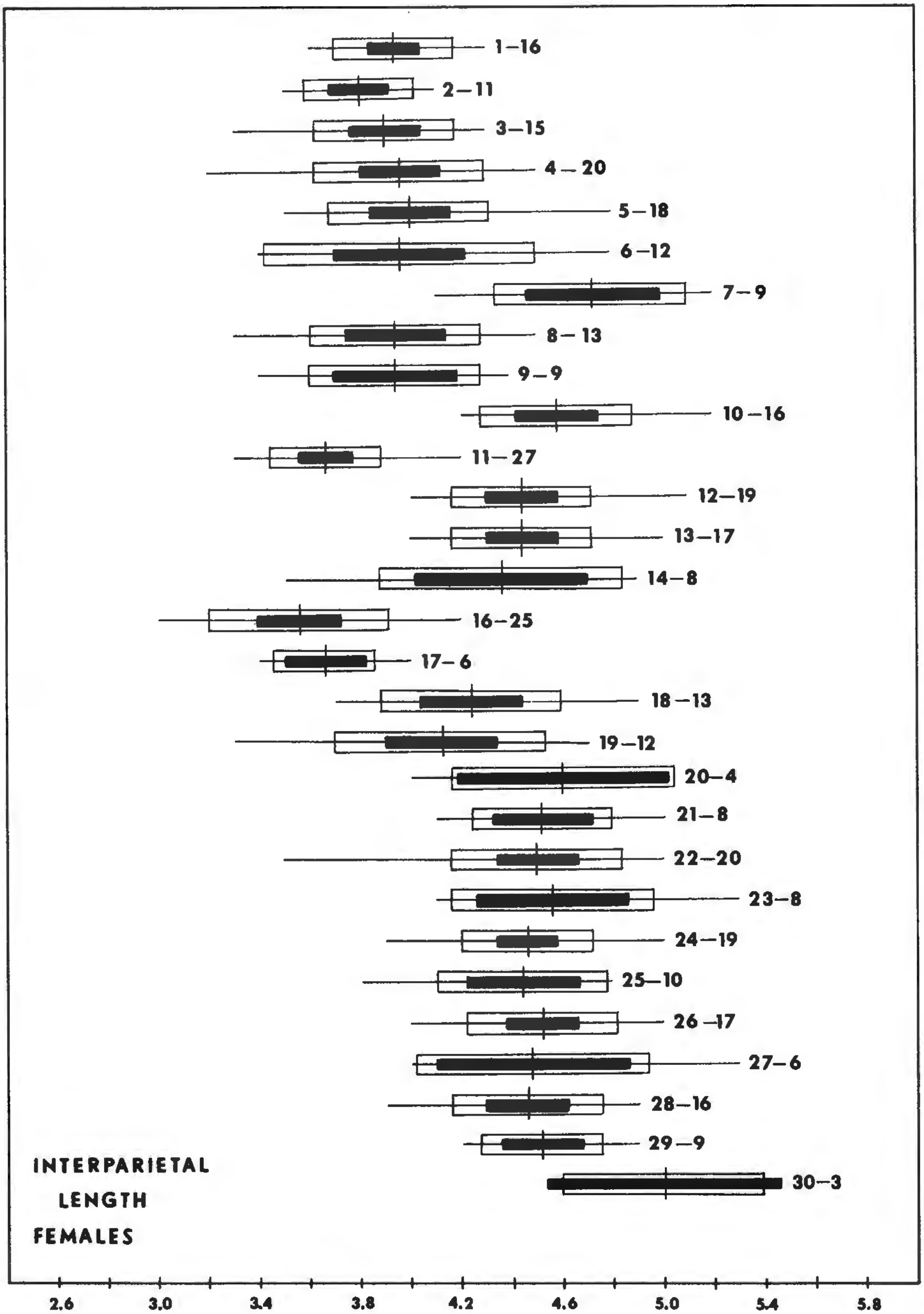

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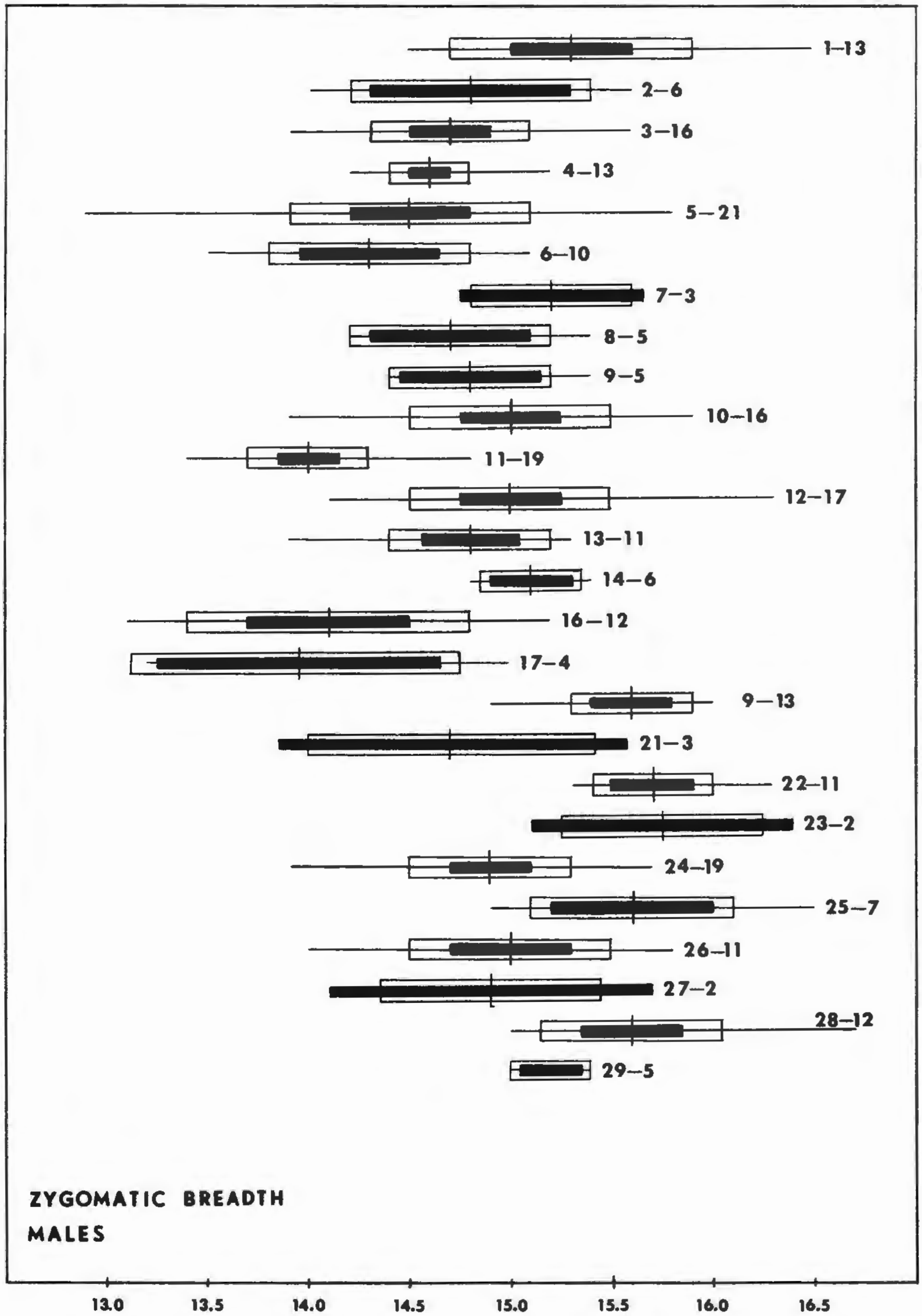

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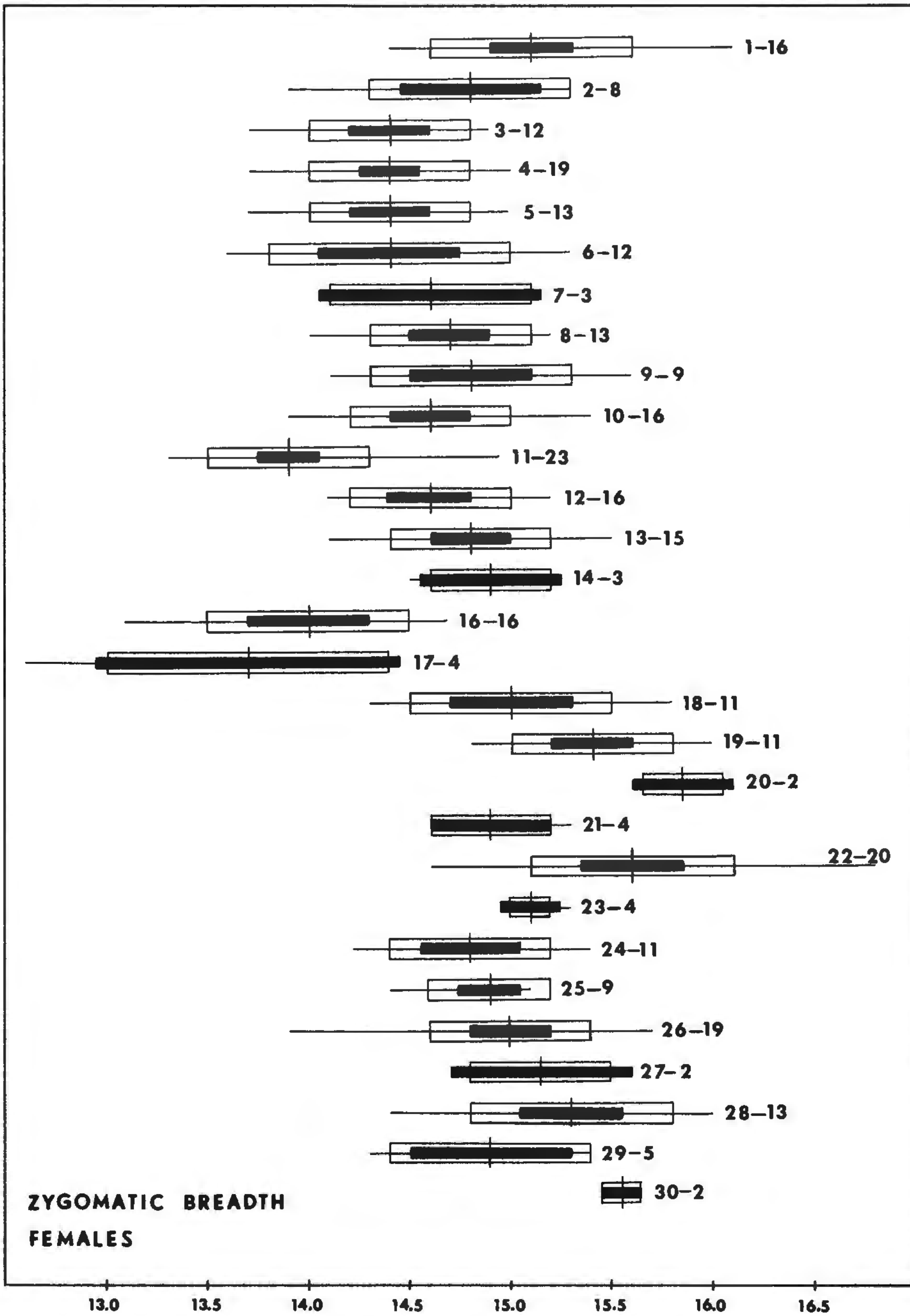

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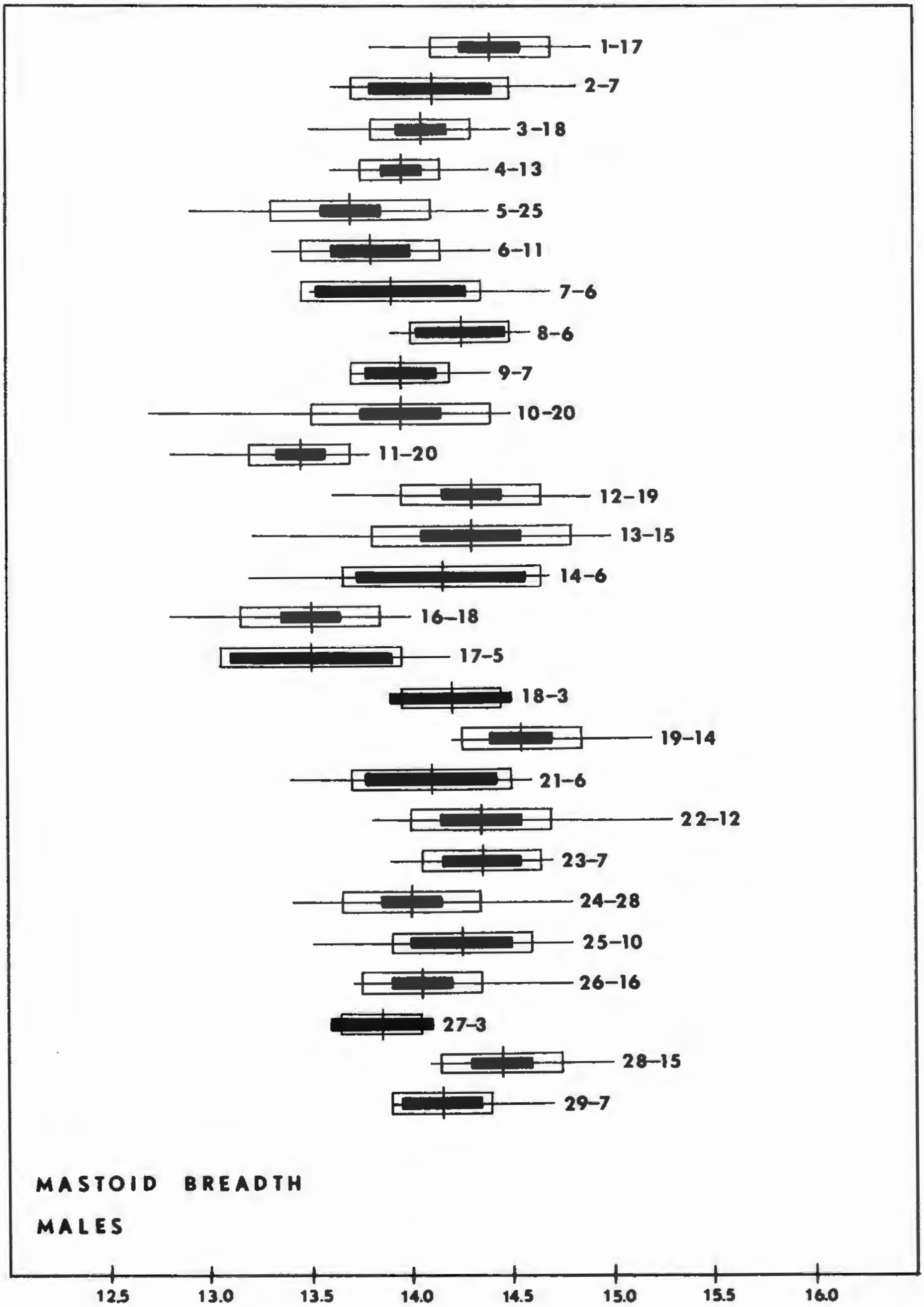

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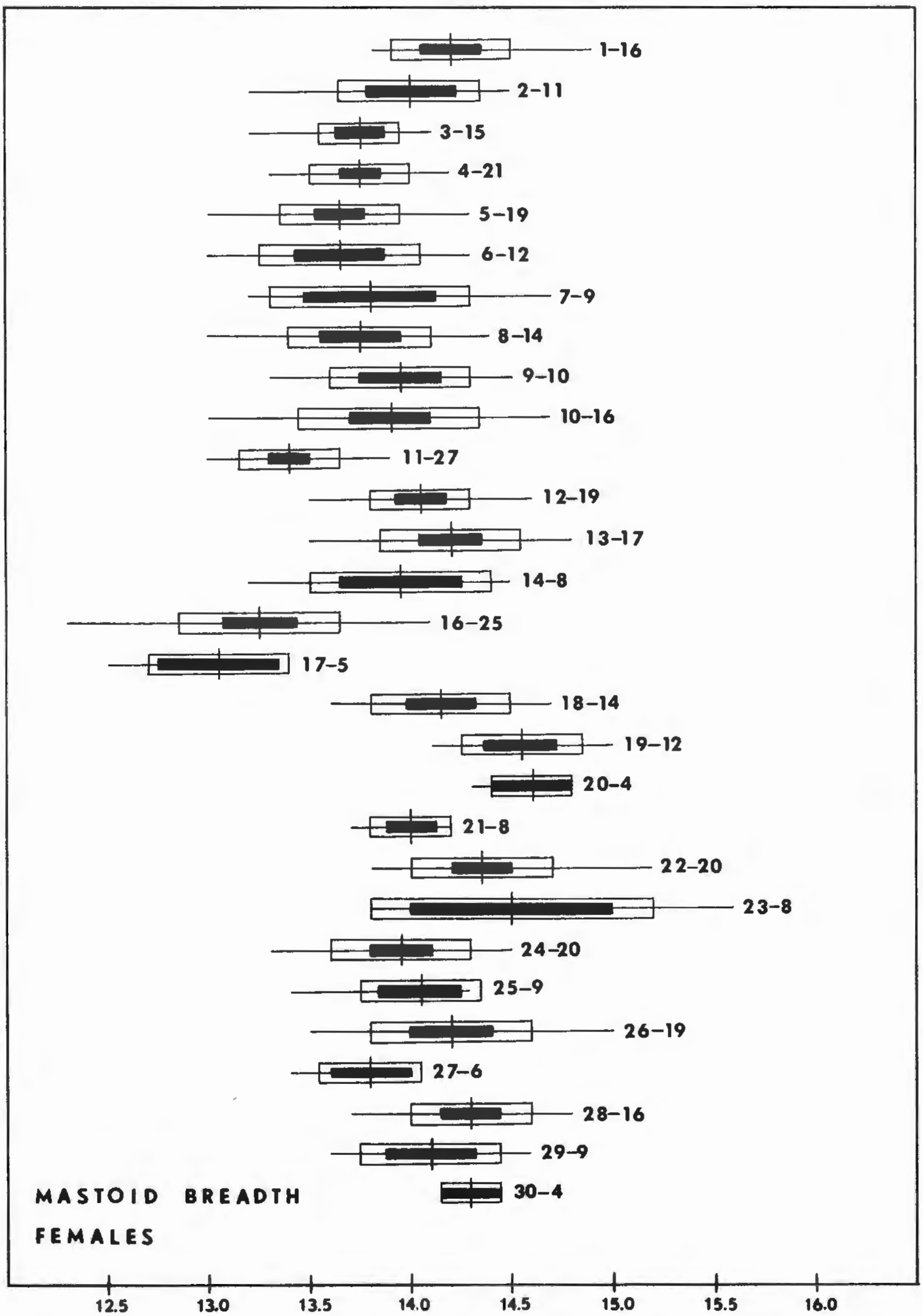

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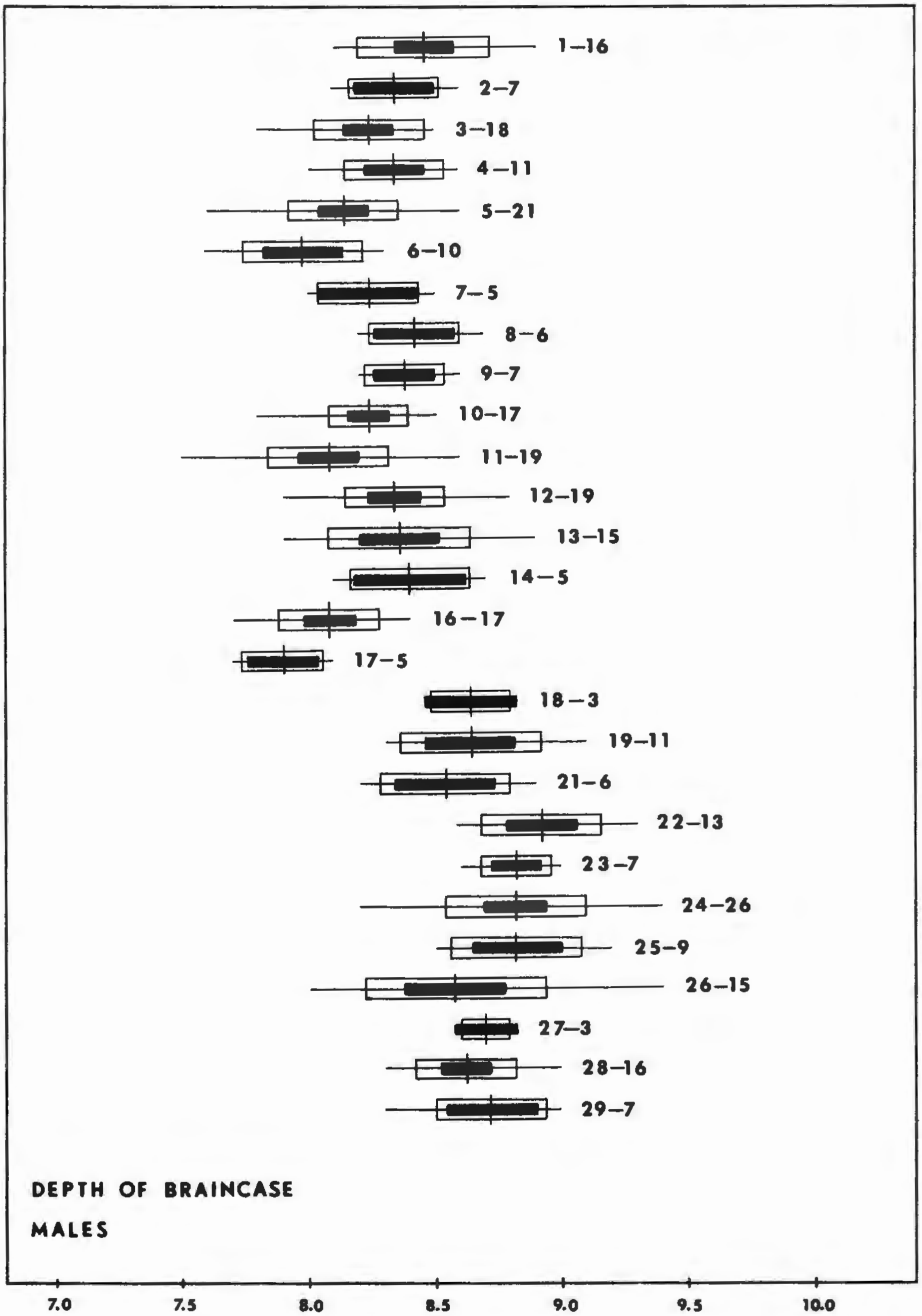

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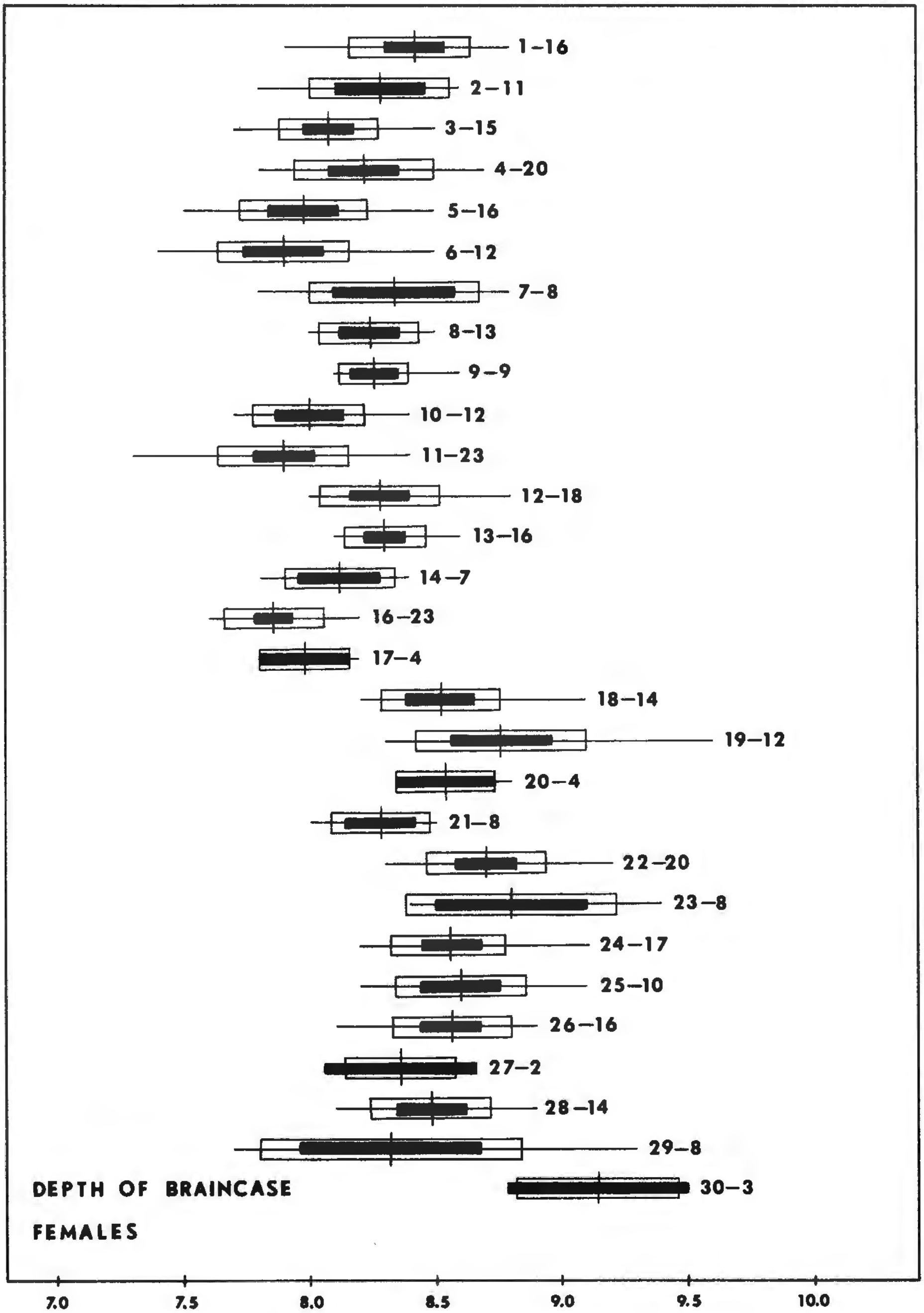


FIG. 20.—Continued.

TABLE 11.—*Geographic variation in external and cranial measurements among 30 samples of* Liomys pictus. *See text for key to sample numbers.*

Sample number	Males				Females			
	N	Mean	Range	2 SE	N	Mean	Range	2 SE
				Total length				
1	14	239.2	211.0-262.0	7.83	14	233.8	221.0-257.0	5.26
2	8	238.1	230.0-251.0	4.99	11	221.7	207.0-244.0	6.60
3	18	226.8	202.0-259.0	5.81	13	217.5	207.0-229.0	3.68
4	9	234.0	220.0-244.0	5.82	15	224.3	205.0-241.0	4.48
5	24	229.6	208.0-265.0	4.70	16	219.8	198.0-232.0	4.52
6	10	217.6	196.0-232.0	6.66	11	214.9	198.0-238.0	7.70
7	6	239.7	231.0-260.0	8.53	7	229.0	217.0-240.0	6.78
8	4	226.8	218.0-239.0	9.71	11	220.5	206.0-232.0	4.80
9	3	228.7	225.0-231.0	3.71	8	226.3	212.0-240.0	6.01
10	22	242.0	226.0-262.0	4.48	18	232.2	210.0-260.0	5.65
11	22	215.5	203.0-239.0	4.39	22	207.3	183.0-240.0	4.75
12	16	238.4	218.0-260.0	6.39	14	225.8	212.0-248.0	5.38
13	10	243.7	232.0-264.0	7.80	14	232.1	220.0-248.0	4.05
14	5	250.2	237.0-270.0	13.56	6	231.0	208.0-251.0	13.41
16	12	218.7	201.0-240.0	6.33	22	211.3	197.0-225.0	3.54
17	4	214.0	207.0-224.0	7.44	5	203.2	195.0-207.0	4.21
18	4	254.0	235.0-267.0	14.12	13	239.2	227.0-253.0	4.16
19	13	241.2	229.0-251.0	3.81	10	239.2	230.0-247.0	3.92
20					4	237.3	219.0-245.0	12.28
21	6	229.3	215.0-240.0	8.92	6	232.2	220.0-240.0	6.08
22	13	263.5	247.0-286.0	5.90	23	249.0	228.0-275.0	5.41
23	5	279.2	260.0-300.0	12.92	6	256.3	242.0-281.0	13.78
24	23	251.1	225.0-289.0	5.76	12	234.8	205.0-246.0	6.59
25	9	262.8	242.0-290.0	10.68	5	239.2	225.0-255.0	10.51
26	14	245.3	220.0-269.0	8.65	19	234.0	218.0-252.0	4.51
27					2	232.5	227.0-238.0	11.00
28	13	237.5	218.0-268.0	8.57	13	220.8	214.0-227.0	2.25
29	9	242.9	221.0-257.0	7.18	9	234.2	216.0-255.0	7.56
30					3	289.7	283.0-294.0	6.77
				Length of tail				
1	14	119.6	91.0-142.0	7.78	14	117.5	110.0-132.0	3.10
2	8	123.1	116.0-137.0	4.62	11	110.5	97.0-132.0	6.15
3	18	116.3	98.0-139.0	4.46	13	112.1	103.0-123.0	3.10
4	9	121.6	113.0-128.0	4.00	15	115.1	105.0-130.0	3.41
5	24	116.5	101.0-138.0	3.16	16	112.6	97.0-125.0	4.05
6	10	108.7	101.0-120.0	3.54	11	110.2	101.0-125.0	4.69
7	6	119.2	107.0-132.0	7.56	8	118.8	110.0-126.0	3.98
8	4	113.0	106.0-117.0	4.97	11	109.7	98.0-118.0	3.67
9	3	113.0	110.0-115.0	3.06	9	113.6	102.0-125.0	4.51
10	22	126.0	105.0-146.0	3.86	18	122.1	110.0-145.0	4.46
11	22	106.0	95.0-120.0	3.27	22	102.8	92.0-124.0	3.25
12	16	122.3	108.0-138.0	4.13	14	116.4	108.0-128.0	3.12
13	11	125.3	117.0-135.0	4.25	15	118.2	110.0-127.0	3.01
14	5	132.4	120.0-152.0	12.14	6	118.8	109.0-132.0	7.03
16	12	111.5	97.0-128.0	5.50	22	108.2	101.0-115.0	2.08

TABLE 11.—*Continued.*

17	4	106.8	105.0-111.0	2.87	5	103.0	98.0-105.0	2.61
18	4	135.5	120.0-145.0	11.68	13	126.5	119.0-141.0	3.29
19	13	117.0	111.0-123.0	2.35	10	119.0	110.0-130.0	3.83
20					4	120.0	103.0-129.0	11.83
21	6	113.5	105.0-123.0	5.95	6	119.5	114.0-123.0	2.77
22	13	135.9	113.0-149.0	5.18	23	128.5	113.0-147.0	3.66
23	5	153.0	140.0-165.0	8.27	7	134.4	122.0-148.0	7.10
24	23	131.3	95.0-149.0	4.46	12	128.4	108.0-139.0	4.53
25	9	142.7	126.0-163.0	8.46	5	128.2	117.0-139.0	8.03
26	14	125.1	100.0-142.0	6.26	19	122.1	106.0-142.0	4.78
27					2	125.5	121.0-130.0	9.00
28	13	117.3	106.0-140.0	5.36	13	110.6	105.0-117.0	1.93
29	9	125.0	112.0-137.0	5.71	9	121.0	111.0-126.0	3.32
30					3	161.3	154.0-168.0	8.11
				Length of hind foot				
1	16	28.6	25.0-32.5	0.93	14	27.7	22.0-30.0	0.97
2	8	27.3	26.0-28.0	0.60	11	27.7	25.0-29.0	0.68
3	20	26.4	24.0-28.0	0.42	15	25.9	23.0-27.0	0.67
4	12	25.8	23.0-28.0	0.86	20	25.8	23.0-28.0	0.56
5	25	26.2	24.0-28.0	0.44	18	26.4	25.0-28.0	0.51
6	11	25.9	23.0-29.0	1.13	13	26.0	24.0-29.0	0.96
7	7	27.1	26.0-28.5	0.70	9	26.8	25.0-28.5	0.78
8	6	26.3	25.0-28.0	0.84	14	26.1	24.0-28.0	0.66
9	4	26.5	26.0-27.5	0.71	9	27.1	26.0-29.0	0.75
10	24	28.9	26.0-30.5	0.44	19	28.4	27.0-31.0	0.48
11	22	25.9	24.5-27.0	0.38	28	25.4	24.0-27.0	0.34
12	19	28.6	27.0-30.0	0.35	19	28.1	26.0-30.0	0.48
13	13	28.7	26.0-31.0	0.97	17	28.6	25.0-31.0	0.89
14	5	29.2	28.0-30.0	0.75	9	27.7	24.0-31.0	1.49
15	2	30.0	29.0-31.0	2.00				
16	16	25.2	23.0-27.0	0.46	23	24.8	23.0-27.0	0.43
17	5	24.0	23.0-25.0	0.63	5	24.2	22.0-25.0	1.17
18	5	29.2	28.0-31.0	1.17	13	28.6	27.0-31.0	0.66
19	16	28.2	27.0-30.0	0.42	12	28.0	25.0-30.0	0.69
20					4	28.8	27.0-30.0	1.50
21	6	28.3	26.0-29.0	0.96	7	28.6	26.0-30.0	1.17
22	13	30.2	28.0-32.0	0.65	24	30.1	28.0-32.0	0.42
23	7	31.1	26.0-33.0	1.87	7	30.9	27.0-35.0	2.11
24	24	28.7	27.0-31.0	0.57	18	28.6	25.0-32.0	0.79
25	10	30.9	28.0-36.0	1.49	8	28.8	26.0-31.0	1.12
26	13	28.7	27.0-31.0	0.65	19	27.5	25.0-30.0	0.55
27					2	25.0	24.0-26.0	2.00
28	17	28.5	26.0-31.0	0.64	16	27.4	25.0-29.0	0.63
29	9	29.0	26.0-30.0	0.88	9	28.9	26.0-32.0	1.31
30					4	34.9	34.5-35.0	0.25
				Greatest length of skull				
1	17	32.3	30.3-34.5	0.58	16	31.8	30.8-34.0	0.43
2	7	31.7	31.2-32.4	0.33	11	31.3	29.9-32.8	0.57
3	17	31.2	30.0-32.7	0.34	14	30.5	29.6-31.5	0.31
4	13	31.0	29.8-32.7	0.49	20	30.6	29.8-31.4	0.19
5	25	30.5	28.6-31.8	0.34	18	30.0	28.1-31.4	0.40
6	11	29.8	27.6-32.4	0.86	12	30.1	27.6-32.1	0.82

TABLE 11.—*Continued.*

7	6	31.8	30.6-32.9	0.64	9	31.6	21.0-32.3	0.35
8	6	31.2	29.7-32.9	1.08	14	30.6	29.4-31.8	0.35
9	7	31.1	30.2-31.8	0.47	9	31.4	30.3-32.8	0.61
10	20	32.1	30.3-33.2	0.33	16	31.7	30.4-32.8	0.40
11	20	30.4	28.9-32.0	0.42	26	29.6	28.0-31.4	0.27
12	19	32.0	30.8-33.5	0.36	18	31.3	30.1-33.0	0.36
13	15	31.9	28.1-34.1	0.74	17	31.7	30.2-32.9	0.29
14	6	32.0	31.1-33.5	0.76	8	31.4	28.5-32.8	1.17
15	2	35.1	34.8-35.4	0.60				
16	17	30.0	28.1-33.2	0.63	22	29.0	26.0-31.5	0.57
17	5	29.1	27.1-30.7	1.20	5	28.4	26.9-29.1	0.78
18	3	33.3	33.0-33.5	0.29	13	32.0	30.6-33.4	0.43
19	12	33.0	32.1-34.6	0.44	12	32.7	31.6-33.4	0.30
20					4	33.0	32.2-34.1	0.84
21	6	32.0	31.4-32.9	0.52	8	31.3	30.3-32.1	0.46
22	13	34.3	32.5-36.7	0.53	20	33.6	31.8-36.0	0.50
23	6	33.2	31.4-34.3	0.90	7	33.3	31.2-35.0	0.92
24	27	32.4	30.8-34.5	0.42	19	31.5	30.4-33.0	0.33
25	9	33.2	31.6-35.0	0.74	10	32.3	31.4-33.7	0.52
26	14	32.7	31.4-34.4	0.48	17	32.0	30.2-33.4	0.44
27	3	31.9	31.3-32.4	0.64	5	31.4	30.8-32.3	0.52
28	16	32.8	31.3-34.6	0.39	15	31.6	30.7-32.7	0.30
29	8	32.6	31.5-33.5	0.54	9	32.1	30.5-34.0	0.76
30					3	34.5	33.7-35.3	0.93
				Zygomatic breadth				
1	13	15.3	14.5-16.5	0.33	16	15.1	14.4-16.1	0.24
2	6	14.8	14.0-15.6	0.51	8	14.8	13.9-15.3	0.33
3	16	14.7	13.9-15.6	0.21	12	14.4	13.7-14.9	0.21
4	13	14.6	14.2-15.2	0.13	19	14.4	13.7-15.0	0.17
5	21	14.5	12.9-15.8	0.28	13	14.4	13.7-15.0	0.20
6	10	14.3	13.5-15.1	0.34	12	14.4	13.6-15.3	0.33
7	3	15.2	14.8-15.6	0.47	3	14.6	14.1-15.0	0.53
8	5	14.7	14.2-15.4	0.42	13	14.7	14.0-15.2	0.20
9	5	14.8	14.4-15.4	0.35	9	14.8	14.1-15.6	0.30
10	16	15.0	13.9-15.9	0.26	16	14.7	13.9-15.4	0.18
11	19	14.0	13.4-14.8	0.16	23	13.9	13.3-14.9	0.17
12	17	15.0	14.1-16.3	0.23	16	14.6	14.1-15.2	0.18
13	11	14.8	13.9-15.3	0.26	15	14.8	14.1-15.5	0.21
14	6	15.1	14.8-15.4	0.20	3	14.9	14.5-15.1	0.37
15	2	15.5	15.2-15.7	0.50				
16	12	14.1	13.1-15.2	0.41	16	14.0	13.1-14.7	0.26
17	4	14.0	13.2-15.0	0.77	4	13.7	12.6-14.3	0.74
18					11	15.0	14.3-15.8	0.29
19	13	15.6	14.9-16.0	0.18	11	15.4	14.8-16.0	0.21
20					2	15.9	15.7-16.0	0.30
21	3	14.7	13.9-15.3	0.85	4	14.9	14.7-15.3	0.29
22	11	15.7	15.3-16.3	0.18	20	15.6	14.6-16.8	0.23
23	2	15.8	15.4-16.1	0.70	4	15.1	15.0-15.3	0.13
24	19	14.9	13.9-15.7	0.20	11	14.8	14.2-15.4	0.26
25	7	15.6	14.9-16.5	0.41	9	14.9	14.4-15.1	0.17
26	11	15.0	14.0-15.8	0.31	19	15.0	13.9-15.7	0.20

TABLE 11.—*Continued.*

27	2	14.9	14.5-15.3	0.80	2	15.2	14.9-15.4	0.50
28	12	15.6	15.0-16.7	0.27	13	15.3	14.4-16.0	0.26
29	5	15.2	15.0-15.4	0.16	5	14.9	14.3-15.4	0.42
30					2	15.6	15.5-15.6	0.10
				Interorbital constriction				
1	17	7.7	7.2-8.5	0.19	16	7.7	7.2-8.3	0.15
2	8	7.4	6.9-7.8	0.20	11	7.5	7.1-8.1	0.21
3	20	7.6	7.2-8.0	0.11	14	7.4	7.0-8.1	0.15
4	14	7.6	6.9-8.1	0.20	21	7.5	7.0-7.9	0.12
5	26	7.4	7.0-8.0	0.11	18	7.5	6.7-8.6	0.20
6	11	7.4	6.7-8.3	0.29	12	7.4	7.0-7.9	0.17
7	7	7.8	7.4-8.3	0.27	8	7.8	7.6-8.3	0.16
8	6	7.7	7.4-8.1	0.20	14	7.4	7.2-7.6	0.07
9	7	7.8	7.4-8.6	0.32	10	7.8	7.5-8.4	0.17
10	22	7.7	7.1-8.2	0.13	19	7.7	7.2-8.5	0.14
11	21	7.3	6.7-7.9	0.12	27	7.1	6.7-7.4	0.07
12	19	7.7	7.1-8.3	0.15	19	7.6	7.1-8.3	0.14
13	15	7.8	6.7-8.7	0.24	18	7.7	6.9-8.6	0.17
14	6	7.8	7.2-8.2	0.30	8	7.7	7.3-8.1	0.24
15	2	7.8	7.7-7.8	0.10				
16	19	7.0	6.6-7.5	0.12	25	6.9	6.3-7.5	0.11
17	5	6.8	6.3-7.0	0.25	5	6.5	6.1-6.9	0.32
18	5	7.7	6.9-8.1	0.44	17	7.6	7.1-8.2	0.15
19	16	7.8	7.1-8.3	0.16	11	7.8	7.4-8.5	0.21
20					4	8.1	7.9-8.6	0.34
21	6	7.6	7.4-8.0	0.18	8	7.3	7.0-7.8	0.19
22	13	8.0	7.6-8.3	0.15	23	7.8	7.1-8.3	0.12
23	7	7.8	7.4-8.5	0.27	8	8.0	7.3-8.8	0.33
24	29	7.8	7.3-8.7	0.14	22	7.7	7.1-8.1	0.13
25	11	7.9	7.3-8.6	0.25	10	7.8	7.1-8.5	0.30
26	16	7.6	7.0-8.5	0.20	20	7.6	6.8-8.1	0.13
27	3	7.8	7.7-8.0	0.20	6	7.8	7.2-8.3	0.35
28	18	7.8	7.2-8.4	0.13	16	7.5	7.1-8.0	0.13
29	9	7.8	7.4-8.4	0.23	9	7.4	7.1-7.8	0.13
30					4	8.0	7.7-8.1	0.19
				Mastoid breadth				
1	17	14.4	13.8-14.9	0.16	16	14.2	13.7-14.9	0.16
2	7	14.1	13.6-14.8	0.31	11	14.0	13.2-14.5	0.22
3	18	14.0	13.5-14.5	0.12	15	13.7	13.2-14.1	0.12
4	13	13.9	13.6-14.4	0.11	21	13.8	13.3-14.2	0.11
5	25	13.7	12.9-14.4	0.15	19	13.7	13.0-14.3	0.13
6	11	13.8	13.3-14.4	0.21	12	13.6	13.0-14.3	0.23
7	6	13.9	13.5-14.7	0.38	9	13.8	13.2-14.7	0.32
8	6	14.3	13.9-14.6	0.22	14	13.8	13.0-14.4	0.20
9	7	13.9	13.7-14.4	0.17	10	13.9	13.3-14.5	0.21
10	20	13.9	12.7-14.5	0.19	16	13.9	13.1-14.7	0.22
11	20	13.5	12.8-13.8	0.12	27	13.4	13.0-13.9	0.09
12	19	14.3	13.6-14.9	0.16	19	14.1	13.5-14.6	0.12
13	15	14.3	13.2-15.0	0.26	17	14.2	13.5-14.8	0.17
14	6	14.2	13.2-14.7	0.42	8	14.0	13.2-14.5	0.31
15	2	14.8	14.7-14.9	0.20				

TABLE 11.—*Continued.*

16	18	13.5	12.8-14.0	0.16	25	13.3	12.3-14.1	0.17
17	5	13.5	13.1-14.2	0.39	5	13.1	12.5-13.3	0.30
18	3	14.2	13.9-14.4	0.31	14	14.2	13.6-14.7	0.18
19	14	14.6	14.2-15.2	0.15	12	14.6	14.1-15.0	0.17
20					4	14.6	14.3-14.8	0.21
21	6	14.1	13.4-14.6	0.33	8	14.0	13.7-14.2	0.13
22	12	14.4	13.8-15.3	0.20	20	14.4	13.8-15.2	0.16
23	7	14.4	13.9-14.7	0.21	8	14.5	13.8-15.6	0.49
24	28	14.0	13.4-14.8	0.14	20	14.0	13.3-14.5	0.15
25	10	14.3	13.5-14.8	0.24	9	14.0	13.4-14.3	0.21
26	16	14.1	13.7-14.8	0.15	19	14.2	13.5-15.0	0.19
27	3	13.9	13.7-14.1	0.24	6	13.8	13.4-14.0	0.19
28	15	14.5	14.1-15.0	0.16	16	14.3	13.7-14.8	0.14
29	7	14.1	13.9-14.7	0.20	9	14.1	13.6-14.6	0.22
30					4	14.3	14.1-14.4	0.14
				Length of nasals				
1	17	12.0	10.3-13.0	0.38	16	12.1	11.4-13.2	0.26
2	8	12.6	11.6-13.3	0.37	11	11.9	11.3-13.1	0.33
3	19	12.0	11.2-12.9	0.22	14	11.6	10.8-12.4	0.28
4	14	11.7	11.0-12.6	0.27	21	11.5	10.8-12.4	0.20
5	25	11.6	10.5-12.2	0.18	18	11.2	10.3-12.2	0.27
6	11	11.5	10.3-13.4	0.58	12	11.5	10.0-12.7	0.49
7	7	12.8	11.8-13.5	0.39	9	12.5	10.8-13.3	0.48
8	6	12.1	11.0-12.8	0.56	14	11.9	10.6-12.5	0.30
9	7	12.1	11.5-13.1	0.40	10	12.0	11.1-12.9	0.37
10	23	13.1	11.7-13.7	0.20	19	12.7	11.9-13.6	0.21
11	22	11.7	10.5-12.8	0.25	27	11.2	10.4-12.2	0.19
12	19	12.9	12.1-13.7	0.25	18	12.5	11.1-13.9	0.32
13	15	12.9	10.8-14.3	0.43	18	12.7	11.8-13.7	0.24
14	6	12.4	11.3-13.3	0.59	9	12.4	10.2-13.3	0.70
15	2	13.7	13.5-13.9	0.40				
16	18	11.5	10.3-12.7	0.33	23	10.9	9.5-12.8	0.33
17	5	11.1	9.9-11.9	0.72	6	11.2	9.6-11.9	0.69
18	5	13.0	12.3-13.8	0.51	17	12.6	11.8-13.4	0.24
19	14	13.4	12.6-14.5	0.32	11	13.1	12.8-13.6	0.17
20					4	13.4	13.1-13.8	0.31
21	6	12.5	12.0-13.1	0.36	8	12.0	11.2-12.9	0.49
22	13	14.1	13.3-15.8	0.40	24	13.9	12.7-15.1	0.29
23	6	13.6	12.7-14.7	0.60	6	13.8	12.6-14.8	0.67
24	24	12.9	11.9-14.2	0.26	21	12.5	11.5-13.7	0.25
25	11	13.5	12.5-14.7	0.36	10	12.9	11.9-13.9	0.36
26	16	13.1	11.6-14.0	0.33	18	12.8	12.0-14.0	0.27
27	3	12.8	12.3-13.1	0.48	6	12.5	11.9-13.2	0.37
28	18	13.2	11.8-14.1	0.24	15	12.6	11.8-13.8	0.30
29	9	13.2	12.4-13.9	0.34	9	12.7	11.9-14.3	0.50
30					3	13.5	12.5-14.1	1.03
				Length of rostrum				
1	16	14.0	12.8-14.8	0.32	16	13.7	13.1-15.1	0.26
2	8	13.8	13.0-14.5	0.30	11	13.4	12.5-14.5	0.39
3	18	13.5	12.7-14.6	0.25	14	13.1	12.6-13.9	0.21

TABLE 11.—*Continued.*

4	14	13.4	12.9-14.3	0.25	21	13.2	12.6-13.7	0.13
5	21	13.2	12.3-14.0	0.22	16	12.9	12.1-13.9	0.28
6	11	12.7	11.2-14.9	0.61	12	13.0	11.8-14.4	0.48
7	6	14.1	13.4-14.9	0.39	5	13.9	13.5-14.4	0.33
8	6	13.5	12.6-14.4	0.56	14	13.3	12.7-14.2	0.23
9	7	13.4	13.0-13.9	0.22	10	13.5	12.9-14.4	0.31
10	17	14.2	13.7-15.0	0.18	13	13.9	13.2-14.8	0.28
11	22	13.0	12.2-13.9	0.20	24	12.6	11.1-13.6	0.24
12	19	14.0	13.0-14.9	0.23	17	13.6	13.0-14.6	0.24
13	14	14.0	12.1-15.5	0.45	16	13.9	13.0-14.6	0.22
14	6	13.9	13.1-14.7	0.46	9	13.8	12.1-14.8	0.63
15	2	15.8	15.5-16.0	0.50				
16	14	13.0	12.0-14.4	0.41	19	12.6	10.9-13.8	0.34
17	4	12.7	12.2-13.4	0.56	5	12.6	12.1-13.1	0.35
18	4	14.6	13.8-15.0	0.54	12	14.0	13.0-14.5	0.30
19	14	14.6	13.8-15.7	0.31	11	14.4	13.9-14.7	0.14
20					4	14.4	14.1-14.8	0.30
21	5	14.1	13.6-14.4	0.30	3	13.7	13.3-14.2	0.53
22	13	15.5	14.6-16.9	0.30	24	15.1	13.9-16.4	0.27
23	4	14.6	13.7-15.8	0.88	6	14.9	14.0-16.1	0.58
24	20	14.4	13.4-15.3	0.26	19	14.2	13.2-16.3	0.32
25	11	14.9	14.0-16.1	0.39	10	14.4	13.8-15.3	0.36
26	16	14.4	12.7-15.4	0.31	17	14.0	13.2-14.9	0.23
27	2	14.0	13.7-14.2	0.50	6	14.1	13.8-14.9	0.33
28	18	14.8	14.0-15.7	0.21	15	14.2	13.4-14.8	0.23
29	8	14.5	13.8-15.0	0.29	9	14.1	13.0-15.8	0.58
30					3	16.3	16.0-17.0	0.67
			Length of maxillary toothrow					
1	16	5.1	4.8-5.5	0.10	16	5.1	4.7-5.5	0.12
2	8	5.1	4.9-5.4	0.11	11	4.9	4.7-5.3	0.12
3	19	4.9	4.5-5.2	0.08	14	4.8	4.5-5.2	0.12
4	14	5.0	4.7-5.2	0.09	20	4.9	4.6-5.2	0.08
5	24	4.8	4.2-5.4	0.10	19	4.8	4.5-5.1	0.07
6	11	4.7	4.5-4.9	0.07	12	4.7	4.4-5.0	0.11
7	6	4.7	4.5-5.0	0.16	9	4.7	4.3-4.9	0.13
8	6	5.1	4.8-5.4	0.18	14	5.1	4.7-5.4	0.09
9	7	5.0	4.5-5.5	0.25	10	5.1	4.8-5.6	0.17
10	22	5.0	4.6-5.6	0.10	15	4.9	4.4-5.3	0.12
11	22	4.8	4.6-5.3	0.08	27	4.8	4.5-5.3	0.07
12	19	4.9	4.7-5.3	0.08	19	4.8	4.4-5.2	0.11
13	13	4.9	4.5-5.4	0.15	18	4.9	4.6-5.1	0.07
14	6	4.8	4.5-5.1	0.22	9	4.8	4.7-5.1	0.09
15	2	5.2	5.1-5.2	0.10				
16	19	4.8	4.3-5.3	0.14	24	4.7	4.3-5.1	0.09
17	5	4.7	4.4-5.0	0.23	6	4.7	4.4-4.9	0.16
18	4	4.8	4.7-4.9	0.10	17	4.9	4.5-5.2	0.09
19	17	5.2	5.1-5.5	0.05	12	5.1	4.9-5.3	0.07
20					4	4.7	4.3-5.0	0.29
21	5	4.9	4.7-5.2	0.18	5	4.7	4.4-4.9	0.17
22	12	5.2	4.7-5.5	0.13	24	5.1	4.9-5.4	0.07
23	6	5.1	4.8-5.3	0.20	8	5.1	4.8-5.7	0.23

TABLE 11.—*Continued.*

24	30	4.8	4.5-5.3	0.07	21	4.8	4.2-5.2	0.13
25	11	5.1	4.6-5.6	0.19	9	4.8	4.5-5.2	0.12
26	17	4.9	4.7-5.1	0.07	19	4.9	4.5-5.5	0.13
27	2	4.8	4.6-4.9	0.30	5	4.9	4.6-5.0	0.15
28	18	4.9	4.3-5.3	0.13	16	4.7	4.4-5.2	0.10
29	9	4.8	4.5-5.3	0.16	9	4.7	4.5-4.9	0.11
30					4	5.3	5.1-5.4	0.14
				Depth of braincase				
1	16	8.5	8.1-8.9	0.13	16	8.4	7.9-8.8	0.12
2	7	8.3	8.1-8.6	0.14	11	8.3	7.8-8.6	0.17
3	18	8.2	7.8-8.5	0.10	15	8.1	7.7-8.5	0.10
4	11	8.3	8.0-8.6	0.12	20	8.2	7.8-8.7	0.13
5	21	8.1	7.6-8.6	0.10	16	8.0	7.5-8.5	0.13
6	10	8.0	7.6-8.3	0.15	12	7.9	7.4-8.5	0.15
7	5	8.2	8.0-8.5	0.19	8	8.3	7.8-8.8	0.24
8	6	8.4	8.2-8.7	0.15	13	8.2	8.0-8.5	0.11
9	7	8.4	8.2-8.6	0.12	9	8.3	8.1-8.6	0.10
10	17	8.2	7.8-8.5	0.08	12	8.0	7.7-8.4	0.13
11	19	8.1	7.5-8.6	0.11	23	7.9	7.3-8.4	0.11
12	19	8.4	7.9-8.8	0.09	18	8.3	8.0-8.8	0.11
13	15	8.4	7.9-8.9	0.15	16	8.3	8.1-8.6	0.08
14	5	8.4	8.1-8.7	0.22	7	8.1	7.8-8.4	0.16
15	2	8.8	8.7-8.9	0.20				
16	17	8.1	7.7-8.4	0.09	23	7.9	7.6-8.2	0.08
17	5	7.9	7.7-8.1	0.14	4	8.0	7.8-8.2	0.17
18	3	8.6	8.5-8.8	0.18	14	8.5	8.2-9.1	0.13
19	11	8.6	8.3-9.1	0.17	12	8.8	8.3-9.6	0.20
20					4	8.6	8.4-8.8	0.19
21	6	8.5	8.2-8.9	0.20	8	8.3	8.0-8.5	0.14
22	13	8.9	8.6-9.3	0.13	20	8.7	8.3-9.2	0.11
23	27	8.8	8.6-9.0	0.10	8	8.8	8.4-9.4	0.29
24	26	8.8	8.2-9.4	0.11	17	8.6	8.2-9.1	0.11
25	9	8.8	8.5-9.2	0.17	10	8.6	8.2-9.1	0.16
26	15	8.6	8.0-9.4	0.19	16	8.6	8.1-8.9	0.12
27	3	8.7	8.6-8.8	0.12	2	8.4	8.2-8.5	0.30
28	16	8.6	8.3-9.0	0.10	14	8.5	8.1-8.9	0.13
29	7	8.7	8.3-9.0	0.17	8	8.3	7.7-9.3	0.36
30					3	9.1	8.9-9.5	0.37
				Interparietal width				
1	17	8.9	8.2-9.4	0.15	16	8.9	7.6-9.7	0.26
2	7	8.7	8.0-9.4	0.41	11	8.9	7.8-9.9	0.33
3	19	8.8	8.1-9.9	0.21	15	8.5	7.7-9.2	0.19
4	12	9.0	8.5-9.7	0.23	20	8.9	7.7-9.6	0.21
5	24	8.8	8.1-9.8	0.16	19	8.7	7.5-9.8	0.22
6	11	8.4	7.5-9.2	0.31	12	8.3	7.6-9.3	0.27
7	6	8.6	8.2-9.2	0.29	9	8.4	6.9-9.0	0.41
8	6	8.8	8.5-9.5	0.31	13	8.7	7.3-9.4	0.30
9	7	8.8	8.3-9.0	0.19	10	8.1	6.7-9.3	0.59
10	20	8.9	8.1-9.7	0.19	15	9.0	7.8-9.9	0.30
11	20	8.3	7.8-8.8	0.12	26	8.3	7.5-8.9	0.13

TABLE 11.—*Continued.*

12	19	8.8	7.9-9.5	0.18	19	8.9	8.1-9.5	0.18
13	15	8.9	8.4-9.6	0.19	17	8.6	7.9-9.5	0.24
14	6	8.6	7.9-9.5	0.56	9	8.8	7.8-9.6	0.34
15	2	8.5	8.3-8.6	0.30				
16	18	8.3	7.8-9.2	0.21	25	8.2	7.5-9.2	0.19
17	5	8.2	7.6-9.0	0.55	6	8.1	7.6-8.6	0.28
18	4	8.9	8.2-9.7	0.63	13	8.5	7.9-9.1	0.17
19	13	8.7	7.9-9.0	0.17	12	8.4	7.2-9.1	0.30
20					4	9.7	9.4-9.9	0.24
21	5	8.8	8.0-9.9	0.65	8	8.7	8.2-9.5	0.29
22	12	9.1	7.9-9.9	0.30	20	9.0	8.4-9.5	0.15
23	7	8.6	7.8-9.0	0.37	8	8.7	7.8-9.6	0.42
24	29	8.9	7.7-9.9	0.21	19	8.9	8.4-9.6	0.18
25	10	9.1	8.5-9.6	0.23	10	8.8	8.4-9.5	0.20
26	15	9.2	8.7-9.9	0.20	17	9.1	8.5-9.9	0.17
27	3	9.0	8.7-9.3	0.35	5	8.7	7.5-9.5	0.73
28	16	9.0	8.5-9.6	0.14	16	8.8	8.1-9.8	0.27
29	7	8.7	7.9-9.1	0.38	9	8.9	8.2-9.9	0.47
30					3	8.8	8.4-9.3	0.55
				Interparietal length				
1	17	4.0	3.6-4.7	0.14	16	3.9	3.6-4.3	0.12
2	7	3.7	3.2-4.2	0.26	11	3.8	3.5-4.1	0.13
3	19	4.1	3.5-4.8	0.15	15	3.9	3.3-4.3	0.14
4	12	4.0	3.5-4.7	0.24	20	4.0	3.2-4.5	0.15
5	24	4.0	3.6-4.4	0.10	18	4.0	3.5-4.8	0.15
6	11	3.9	3.3-4.6	0.28	12	4.0	3.4-4.8	0.31
7	6	4.7	4.4-5.2	0.24	9	4.7	4.1-5.2	0.25
8	6	3.9	3.5-4.3	0.24	13	3.9	3.3-4.5	0.19
9	7	4.2	3.9-4.6	0.19	9	3.9	3.4-4.4	0.23
10	20	4.6	4.1-5.2	0.12	16	4.6	4.2-5.2	0.15
11	21	3.8	3.4-4.5	0.13	27	3.7	3.3-4.2	0.09
12	19	4.4	3.8-5.1	0.13	19	4.4	4.0-5.1	0.13
13	15	4.6	4.1-5.1	0.16	17	4.4	4.0-5.0	0.13
14	6	4.5	4.1-5.0	0.27	8	4.4	3.5-4.9	0.33
15	2	4.7	4.5-4.8	0.30				
16	18	3.6	3.2-4.7	0.18	25	3.6	3.0-4.2	0.15
17	5	3.7	3.5-4.0	0.18	6	3.7	3.4-4.0	0.16
18	5	4.3	3.9-4.5	0.22	13	4.2	3.7-4.9	0.20
19	13	4.1	3.6-4.7	0.17	12	4.1	3.3-4.7	0.24
20					4	4.6	4.0-5.0	0.43
21	6	4.4	4.0-4.8	0.22	8	4.5	4.1-5.0	0.19
22	13	4.7	4.2-5.3	0.17	20	4.5	3.5-5.0	0.15
23	7	4.5	4.1-5.3	0.30	8	4.6	4.1-5.3	0.29
24	29	4.6	3.7-5.5	0.17	19	4.5	3.9-5.0	0.12
25	10	4.5	3.8-4.8	0.25	10	4.4	3.8-4.8	0.21
26	15	4.3	3.8-4.9	0.17	17	4.5	4.0-5.0	0.14
27	3	4.7	4.3-5.4	0.68	6	4.5	4.0-5.3	0.38
28	17	4.6	3.8-5.3	0.19	16	4.5	3.9-4.9	0.15
29	7	4.7	4.0-5.2	0.30	9	4.5	4.2-4.9	0.16
30					3	5.0	4.6-5.4	0.46

Cranial Measurements

The 10 cranial measurements will be discussed below in the order they were for *Liomys irroratus*—1) measurements of cranial length; 2) measurements of cranial breadth; 3) measurement of cranial depth.

A smooth cline is shown in the mean greatest length of skull of specimens from northwestern México (Fig. 20 and Tables 11, 12). In these, there is a decrease in size from the medium-sized specimens of sample 1 in the north to the relatively small specimens of sample 6 in the south. Specimens from sample 7, as they did in total length, average considerably larger than specimens from sample 6 and more nearly approach specimens from samples 10 and 12 to 14 to the south. Males and females from sample 8 and the males from sample 9 have a greatest length of skull that averages intermediate between the smaller animals to the north (6) and larger to the west (7). However, females from sample 9 are relatively large and more nearly approach specimens from sample 10. The means for specimens from interior Jalisco, Michoacán, and Guerrero (samples 11, 16, 17) become progressively smaller to the south, with specimens from sample 17 averaging the smallest of the species. Mice from the Sierra Madre del Sur of Guerrero and Oaxaca (samples 20, 22, 23, 30) are relatively large; this is especially noticeable in the mean greatest length of skull for females. Only males from southeastern Oaxaca and northwestern Chiapas (sample 25) approach them in size. It should be noted that the last sample (25) is the only area where the geographic ranges of *Liomys pictus* and *Liomys salvini* are sympatric. Some specimens from the vicinity of San Gabriel Mixtepec, Oaxaca (22), reach the largest size of the species, although the three females from Omilteme, Guerrero (30), average largest. It is interesting to note that specimens from sample 20 more nearly agree with specimens from the montane area rather than the coastal areas as they did in external measurements. Excepting the three rather large males from sample 18 and the relatively small specimens (as they were externally) from sample 21, the other specimens form a group having skulls of medium length that does not appear to be appreciably different from that of specimens in western Jalisco and Colima. One last point of interest is that females from the Pacific slopes of Sierra Madre in Guerrero (sample 19) are somewhat larger than females from adjacent lowlands (18) as might be expected from their intermediate geographic position between the coastal and montane populations.

Variation in length of nasals (Fig. 20 and Table 11) for populations of *Liomys pictus* from throughout the range of the species agrees closely with the pattern for greatest length of skull. Samples 1 to 6 show a clinal decrease in size from north (1) to south (6) except that males from sample 1 have, on the average, shorter nasals than do males from sample 2, and females from sample 5 are the smallest of the group. The mean length of nasals for specimens from sample 7 is long and appears to fall into a group characterized by nasals of medium length that includes specimens from samples 10, 12 to 14, 18, 19, 21, and 24 to 29. Mice from samples 11, 16, and 17, again, form a group characterized by small size. Specimens from samples 20, 22, 23, and 30 have, on the average, the longest nasals of the species. The mean length of nasals for specimens of both sexes from sample 19 is intermediate between the mean for coastal and montane populations as is the geographic location. Specimens from sample 21 average smaller than those from surrounding samples but still fall within the lower end of variation for specimens from samples in this group, and males from sample 25 are larger than those from surrounding areas but the females are not.

There are only minor differences in the pattern of variation for length of the rostrum (Table 11) as compared with that for length of nasals. The rostrum of males from sample 19 is no longer than that of males from coastal areas of Guerrero (18). The mean length of rostrum for females from samples 19 and 20 is intermediate between the smaller specimens from sample 18 and larger specimens from samples 22 and 23; however, they do not approach the mean of specimens from sample 30. The males from the montane sample 23 more closely resemble those of adjacent lowland samples in length of rostrum than they resemble animals from the montane sample to the west (22).

The length of the maxillary toothrow (Table 11) does not display a pattern of variation similar to the three previous measurements of length and, in fact, shows little significant variation at all. Specimens from northwestern México show a slight decrease in mean length of maxillary toothrow from samples 1 to 6 and it should be noted that mean for each sex at sample 7 is the same as those for sample 6. The means for specimens from samples 8 and 9 are longer than for mice from sample 10. The only populations south of sample 10 having a mean length of maxillary toothrow of 5.0 or more are 19, 22, 23, and males from sample 25. Only at sample 17 do males have a mean of 4.7 and only at samples 16, 17, 20, 21, 28, and 29 do females have a mean of 4.7. The remainder of the samples have a mean of either 4.8 or 4.9.

The length of interparietal bone (Fig. 20 and Tables 11, 12) averages almost uniformly a medium length for the specimens in samples from northwestern México (1-6), only males from sample 2 being small. Both sexes from sample 8 and females from sample 9 have interparietal bones that average the same length as populations to the north (1-6). Males from sample 9 have a mean length of interparietal that is intermediate between the samples to the west and south (7, 10, 12, 14) with long interparietal bones and the samples to the north (1-6) with interparietals of medium length. Samples 11, 16, and 17 have a short interparietal bone, with specimens from sample 16 having the shortest of the species. The remaining samples including those from montane areas are made up of specimens characterized by long interparietal bones. The three specimens from Omilteme, Guerrero (30), are at the upper end of the range of this variation. Specimens from samples 18 and 19, especially the latter, are somewhat smaller than might be expected in mice from those areas, judging by other mensural data.

Although variation in zygomatic breadth follows the same general pattern of variation as the measurements of cranial length, it is not so variable as the length measurements (Fig. 20 and Table 11). Zygomatic breadth of males from samples 1 to 6 varies clinally. The males from sample 1 have a zygomatic breadth that is in the intermediate range of variation of the species; mean values become progressively smaller to the south until at sample 6 the individuals are on the average

TABLE 12.—*Results of three typical SS-STP analyses (greatest length of skull, mastoid breadth, and interparietal length) of geographic variation of* Liomys pictus. *Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
			Greatest length of skull		
15	35.1		30	34.5	
22	34.3		22	33.6	
18	33.3		23	33.3	
23	33.2		20	33.0	
25	33.2		19	32.7	
19	33.0		25	32.3	
28	32.8		29	32.3	
26	32.7		18	32.0	
29	32.6		26	32.0	
24	32.4		1	31.8	
1	32.3		13	31.7	
10	32.1		10	31.7	
12	32.0		28	31.6	
21	32.0		7	31.6	
14	32.0		24	31.5	
13	31.9		27	31.4	
27	31.9		14	31.4	
7	31.8		9	31.4	
2	31.7		2	31.4	
3	31.2		12	31.3	
8	31.2		21	31.3	
9	31.1		4	30.6	
4	31.0		8	30.6	
5	30.5		3	30.5	
11	30.4		6	30.1	
16	30.0		5	30.0	
6	29.8		11	29.6	
17	29.1		16	29.0	
			17	28.4	
			Mastoid breadth		
15	14.8		20	14.6	
19	14.6		19	14.6	
28	14.5		23	14.5	
1	14.4		22	14.4	

TABLE 12.—*Continued.*

22	14.4	30	14.3
23	14.4	28	14.3
13	14.3	13	14.2
12	14.3	1	14.2
25	14.3	26	14.2
8	14.3	18	14.2
18	14.2	29	14.1
14	14.2	12	14.1
29	14.1	25	14.0
21	14.1	2	14.0
2	14.1	21	14.0
26	14.1	24	14.0
3	14.0	14	14.0
24	14.0	9	13.9
4	14.0	10	13.8
10	13.9	27	13.8
9	13.9	7	13.8
7	13.9	4	13.8
27	13.9	8	13.8
6	13.8	3	13.8
5	13.7	5	13.7
17	13.5	6	13.6
16	13.5	11	13.4
11	13.5	16	13.3
		17	13.1

Length of interparietal

27	4.7	30	5.0
29	4.7	7	4.7
7	4.7	20	4.6
22	4.7	10	4.6
15	4.7	23	4.6
24	4.6	21	4.5
28	4.6	26	4.5
10	4.6	29	4.5
13	4.6	22	4.5
14	4.5	27	4.5
25	4.5	24	4.5
23	4.5	28	4.5
12	4.4	12	4.4
21	4.4	25	4.4
18	4.3	13	4.4
26	4.3	14	4.4
9	4.2	18	4.3

TABLE 12.—*Continued.*

19	4.2	19	4.1
3	4.1	5	4.0
1	4.0	6	4.0
4	4.0	4	4.0
5	4.0	1	3.9
6	3.9	9	3.9
8	3.9	8	3.9
11	3.8	3	3.9
2	3.7	2	3.8
17	3.7	17	3.7
16	3.6	11	3.7
		16	3.6

relatively small. Males from the vicinity of San Blas, Nayarit (sample 7), are much larger than males from northern Nayarit (6) and more closely resemble males from southwestern Nayarit and western Jalisco (10, 12-14). Males from samples 8 and 9 have zygomatic breadths that average between the values of the small males from sample 6 and the larger males from sample 7. Females from these areas show a different pattern of variation. Females from samples 1 and 2 are larger than those to the south as were the males, but the females from samples 3 to 6 have the same average zygomatic breadth. Although females from samples 7 to 10 have a somewhat greater zygomatic breadth than those to the north (3-6), it is certainly not a striking difference that causes a sharp break in the variation as it does in males. Specimens from samples 11, 16, and 17 form a unit characterized by a narrow mean zygomatic breadth; this is more readily seen in females than in males. Another unit characterized by a broad mean value is formed by the montane samples from Oaxaca and Guerrero (20, 22, 23, 30). The females from sample 23 are relatively small but the sample contains only four individuals. Males from samples 25 and 28 and to some extent the females from sample 28 (Los Tuxtlas, Veracruz) have a mean zygomatic breadth that is broader than that of adjacent populations. The specimens from sample 19 again show a size that is intermediate between coastal and montane samples. The remaining samples (12-14, 18, 21, 24, 26, 27, 29, and females from 25) have a mean zygomatic breadth that is medium in width for the species and most nearly approaches the condition found in specimens from sample 10. This group forms a chain of samples along the west coast of México and across the Isthmus of Tehuantepec into Veracruz and Chiapas in which the zygomatic breadth is of relatively the same size and exhibits no sharp breaks in the variation.

Specimens from Sonora, Sinaloa, Durango, and northern Nayarit (samples 1-6) show a relatively smooth clinal decrease in mean mastoid breadth from north to south; unlike the case in many other measurements the specimens from sample 7 are not appreciably larger than those from sample 6 (Fig. 20 and Tables 11, 12).

The specimens from this entire area have an average mastoid breadth that is in the middle of the range of variation for the species. The means for samples 5 and 6 are the smallest in this northern group, but the mean mastoid breadths for specimens from samples 11, 16, and 17 are the smallest of the species. Other samples having a mean mastoid breadth that is in the medium size range for the species include 8 to 10, 12 to 14, 18, 21, 24 to 27, 29, and 30. Specimens from the mountains of Oaxaca (20, 22, 23) and the Pacific slope of the Sierra Madre del Sur of Guerrero (19) have, on the average, the broadest mastoid breadth of the species, although the difference between them and the coastal populations is relatively small. Both males and females from Los Tuxtlas, Veracruz (28), have a mean mastoid breadth that is greater than the mastoid breadth of surrounding samples and falls within the range of values of animals in montane areas of Oaxaca and Guerrero.

Variation in the mean breadth of the interorbital constriction along the northwestern coast of México (samples 1-6) shows a clinal decrease in size from north to south with the exception of males from sample 2 and females from sample 3, which have the same means as specimens of their respective sex from sample 6 (Table 11). The specimens from sample 7 have a broad interorbital region and more nearly resemble specimens from southwestern Nayarit, western Jalisco, and Colima (samples 10, 12-14). Also specimens from samples 8 and 9 excepting females from sample 8, which are as small as females from sample 6, have, on the average, an interorbital constriction that more closely approaches that of samples from western Jalisco and Colima (10, 12-14) than those to the north (6). Specimens from the interior of Jalisco, Michoacán, and Guerrero reveal a cline in mean breadth of interorbital constriction from the largest of the group, sample 11 (however, these mice average less than any others except those in this group), to sample 17 (smallest interorbital constriction of the species). The remaining samples with only a few exceptions have specimens with a mean interorbital constriction that is nearly the same. Females from samples 20, 23, and 30 and males from sample 22 have an interorbital constriction that averages 8.0 or more, which is broader than specimens from other samples. Females from samples 28 and 29 have a mean interorbital constriction that is narrower than for females from adjacent samples, but males from these two samples do not show the narrowing of the interorbital region.

Besides the relatively narrow mean interparietal width of specimens from samples 6, 11, 16, and 17 and relatively broad mean interparietal width of specimens from sample 20, the samples of *Liomys pictus* have mean interparietal widths that reveal little variation (Table 11). Females from samples 7 and 9 have an interparietal width that is small, but males from these samples are similar to males from surrounding samples.

The mean depth of braincase varies clinally in specimens from along the northwestern coast of México, those from sample 1 being deeper than those from sample 6 (Fig. 20 and Table 11). Only specimens from high altitudes in Sinaloa and Durango (4) are slightly shallower than would be expected at that point in the cline. Specimens from samples 7, 8, and 9 have crania that average deeper than

TABLE 13.—*Geographical variation in the configuration of the interparietal bone of* Liomys pictus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Interparietal bone			Posterior margin of interparietal bone			
Sample	N	Undivided	Divided	N	Notched	Slightly notched	Unnotched
1	52	48.1	51.9	52	75.0	11.5	13.5
2	39	38.5	61.5	40	80.0	10.0	10.0
3	30	46.7	53.3	31	71.0	22.6	6.4
4	33	42.4	57.6	32	78.1	9.4	12.5
5	70	44.3	55.7	81	81.5	9.9	8.6
6	32	71.9	28.1	33	66.7	12.1	21.2
7	24	100.0	0	24	0	25.0	75.0
8	16	56.3	43.7	24	58.3	12.5	29.2
9	43	62.8	37.2	43	60.5	23.2	16.3
10	52	100.0	0	52	13.5	23.1	63.4
11	72	79.2	20.8	82	85.4	6.1	8.5
12	65	100.0	0	60	18.3	21.7	60.0
13	35	100.0	0	38	7.9	13.2	78.9
14	8	100.0	0	7	14.3	0	85.7
15	3	100.0	0	3	33.3	0	66.7
16	26	96.2	3.8	46	58.7	10.9	30.4
17	9	100.0	0	9	33.3	44.5	22.2
18	10	100.0	0	12	25.0	16.7	58.3
19	28	100.0	0	31	19.4	16.1	64.5
20	3	100.0	0	8	0	37.5	62.5
21	13	100.0	0	19	31.6	21.0	47.4
22	52	98.1	1.9	60	68.3	10.0	21.7
23	23	100.0	0	23	39.1	8.7	52.2
24	13	100.0	0	30	46.7	20.0	33.3
25	7	100.0	0	21	66.7	9.5	23.8
26	22	100.0	0	24	50.0	20.8	29.2
27	9	100.0	0	9	55.6	33.3	11.1
28	38	100.0	0	38	65.8	7.9	26.3
29	22	95.5	4.5	22	13.7	22.7	63.6
30	4	100.0	0	4	0	0	100.0

those from sample 6 and more nearly approach males from samples 10 and 14 and both sexes from samples 12 and 13. The females from samples 10 and 14 have relatively shallow crania and approach specimens from samples 11, 16, and 17, which are the shallowest of the species. The mean depth of braincase for specimens from sample 18 is deeper than for specimens to the north and more nearly approaches that in specimens to the south. The remainder of the samples show little significant variation in the depth of braincase. Specimens from sample 21 average smaller than those from contiguous samples and specimens from Omilteme, Guerrero (sample 30), have, on the average, the deepest braincases of the species.

Qualitative Cranial Characters

Condition of interparietal bone (Table 13).—The longitudinal division of the interparietal bone appears to be characteristic of populations from Sonora, Sinaloa, Durango, the lowlands of northern Nayarit (samples 1-6), inland at higher altitudes in the vicinity of Tepic, Nayarit (8), and Guadalajara, Jalisco (9), and the interior drainage basins of Jalisco (11). In these areas as many as 50 per cent or more of the individuals may show the condition. Only three in-individuals from other samples were found to have the interparietal bone divided; one of these was from sample 16, which is the contiguous sample to the east and south of sample 11, and the other two were from samples 22 and 29.

Notching (large or small) of the posterior margin of the interparietal bone is characteristic of specimens from northwestern México (samples 1-6), inland in the vicinity of Tepic, Nayarit, and Guadalajara, Jalisco (samples 8, 9), and interior Jalisco, Michoacán, and Guerrero (samples 11, 16, 17); in these areas almost 70 per cent or more of the individuals show some kind of notching. Also specimens from Oaxaca, Chiapas, and southern Veracruz (samples 21-28) show notching at least in 50 per cent of the individuals and usually in more than 70 per cent. Samples from the localities in western México from southern Nayarit through Guerrero (samples 7, 10, 12-15, 18, 19, 30), and in eastern México (central Veracruz, sample 29) have a high percentage of the individuals, more than 60 per cent, that do not have a notch in the posterior margin of the interparietal bone.

Condition of posterior nasal region (Table 14).—Most individuals of *Liomys pictus* have an emarginate posterior margin of the nasals. Specimens from samples 7, 10, 18, and 19 do have a high percentage (46.7-86.2) of individuals that have a truncate posterior margin of the nasals, and samples 20, 23, 27, and 28 have more than 20 per cent of the individuals with truncated nasals.

The condition in which the premaxillary bones terminate at the same level as the nasals (no longer than nasals) presents an interesting pattern of variation in northwestern México (samples 1-6). No more individuals from Sonora and northern Sinaloa have the premaxillaries and nasals of equal length than is commonly found elsewhere in the species; southward from sample 1, however, an increasing number of individuals exhibit this condition reaching the highest percentage in sample 4 (86.4 per cent). A high percentage of individuals with the premaxillaries and nasals of equal length is found also in specimens from the vicinity of Tepic, Nayarit, and Guadalajara, Jalisco. In the remaining samples, individuals with the premaxillary bones extending posterior to the nasal bones (longer than the nasals) predominate, although 25 per cent or more of the individuals from samples 22, 23, and 26 have the bones of equal length.

TABLE 14.—*Geographical variation in bones of the posterior portion of the nasal-premaxillary complex of* Liomys pictus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Shape of posterior margin of nasals				Length of premaxillary bones		
Sample	N	Emarginate	Rounded	Truncate	N	Longer than nasals	Equal to nasals
1	51	98.0	2.0	0	51	94.1	5.9
2	39	97.4	2.6	0	39	84.6	15.4
3	31	93.5	6.5	0	30	76.7	23.3
4	35	85.7	14.3	0	34	14.7	86.3
5	73	93.2	6.8	0	82	36.6	63.4
6	33	78.8	15.1	6.1	32	59.4	40.6
7	24	0	37.5	62.5	24	100.0	0
8	24	79.2	12.5	8.3	24	37.5	62.5
9	42	85.7	4.8	9.5	43	18.6	81.4
10	52	15.4	21.1	63.5	52	98.1	1.9
11	81	95.1	4.9	0	84	100.0	0
12	64	60.9	28.2	10.9	64	82.8	17.2
13	36	58.3	25.0	16.7	35	88.6	11.4
14	8	62.5	25.0	12.5	8	87.5	12.5
15	3	100.0	0	0	3	66.7	33.3
16	47	85.1	10.6	4.3	47	100.0	0
17	9	77.8	22.2	0	9	88.9	11.1
18	15	40.0	13.3	46.7	15	93.3	6.7
19	29	6.9	6.9	86.2	32	96.9	3.1
20	8	62.5	12.5	25.0	8	100.0	0
21	19	84.2	15.8	0	19	94.7	5.3
22	61	80.3	8.2	11.5	61	73.8	26.2
23	24	70.8	4.2	25.0	24	62.5	37.5
24	33	87.8	6.1	6.1	36	100.0	0
25	21	90.4	4.8	4.8	21	100.0	0
26	25	92.0	8.0	0	25	64.0	36.0
27	9	66.7	11.1	22.2	9	100.0	0
28	39	56.4	15.4	28.2	39	100.0	0
29	22	72.7	22.7	4.6	22	95.5	4.5
30	4	100.0	0	0	4	100.0	0

Multivariate Analysis

Means of the 13 external and cranial measurements and four qualitative cranial characters were used in the NT-SYS multivariate analysis programs. Phenograms diagraming the phenetic relationships of both male and female *Liomys pictus* were computed from both distance and correlation matrices; the

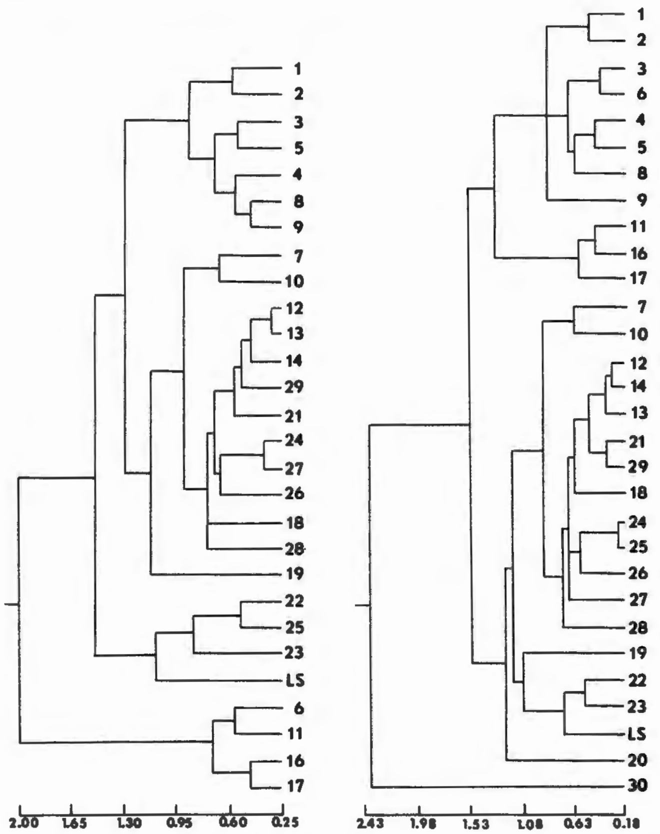


FIG. 21.—Phenograms of numbered samples (see Fig. 19 and text) of *Liomys pictus* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram for males is 0.749 and for females is 0.800. The samples labeled LS are composed of specimens of *Liomys spectabilis*.

phenograms based upon the distance matrix are presented herein because they had larger coefficients of cophenetic correlation (Fig. 21). In addition, a map (Fig. 22), which includes values for both sexes, is presented showing the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components were computed from the matrix of correlation among the 17 characters; these first three components combine to express 82.60 per cent of phenetic variation in males and 81.40 per cent in females. Two-dimensional plots of principal components I-II and I-III and three-dimensional projections of the 30 samples onto the first three principal components based on the matrix of correlation among characters are presented for both sexes (Figs. 23-26).

The distance phenogram for males shows the samples falling into four major clusters. The first cluster includes samples 1 to 5, 8, and 9. This, excepting sample 6, represents the specimens from the coast of northwestern México and

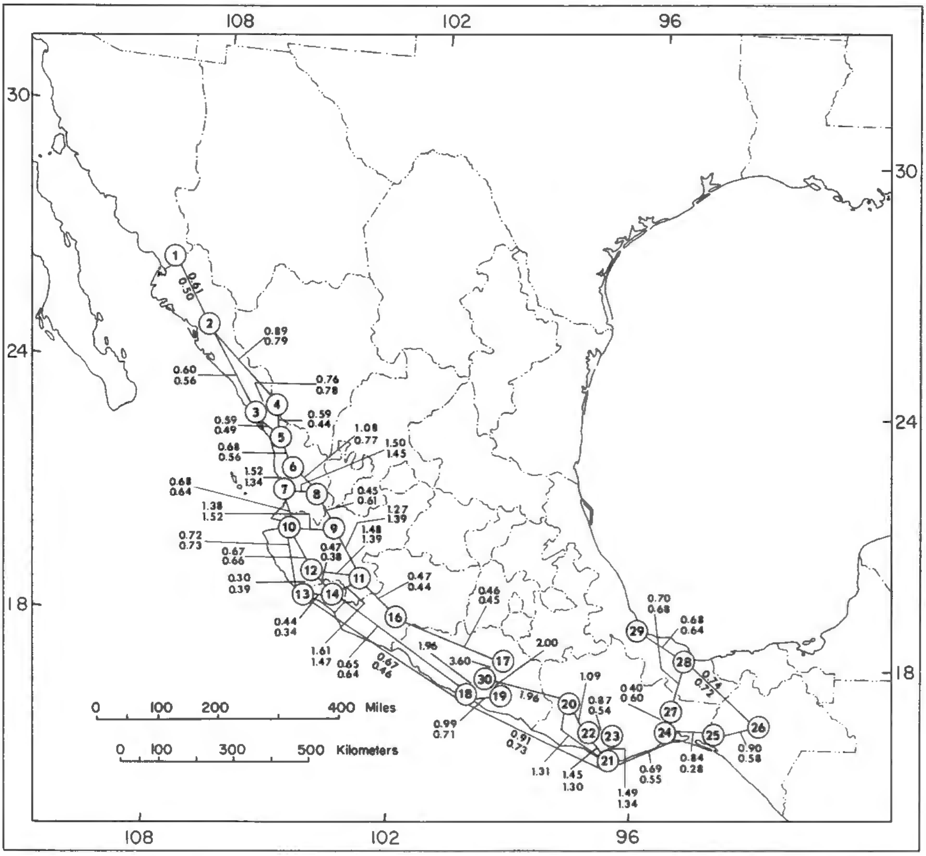
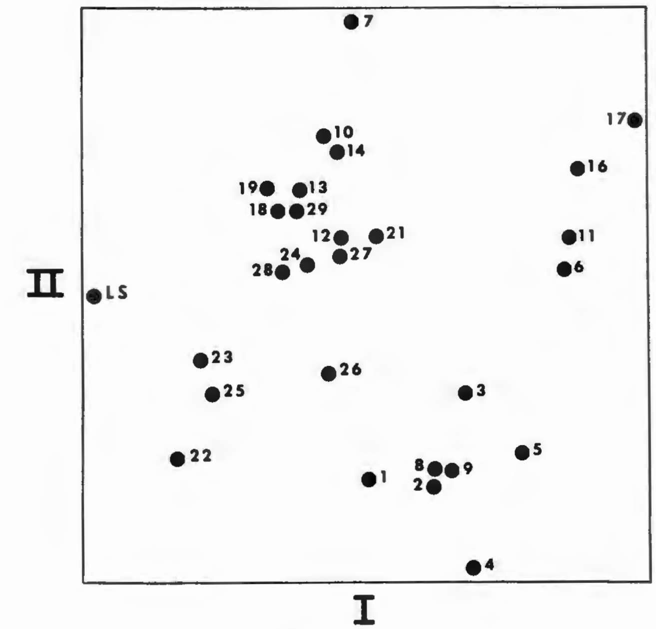


FIG. 22.—Map showing selected distance coefficients (from distance matrices) between samples of *Liomys pictus* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 19 and text for key to samples.

extends inland around Tepic, Nayarit, to the vicinity of Guadalajara, Jalisco. Specimens from northern Nayarit (6) were always found to be small in the univariate analysis and they are grouped with samples 11, 16, and 17, which contain the other small specimens of the species. This grouping, however, is untenable on geographic grounds. Specimens from samples 1 and 2 were usually found to average larger than specimens from other samples in this group and they appear to be phenetically the most distinct. The second cluster includes samples 7, 10, 12 to 14, 18, 19, 21, 24, and 26 to 29. This group includes specimens from along the coast of western México from as far north as San Blas, Nayarit, southward to the Isthmus of Tehuantepec and the interior valley of Chiapas and then northward in the lowland of southern and central Veracruz. Sample 19 shows the greatest distance from other members of this group, which probably can be explained by the tendency of specimens from this sample to be intermediate between coastal and montane samples in measurements in the univariate analysis.

TABLE 15.—*Factor matrix from correlation among 17 characters of* Liomys pictus *studied.*

Character	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Total length	−0.922	−0.088	0.137	−0.935	−0.151	−0.215
Length of tail	−0.820	−0.089	0.304	−0.875	−0.086	−0.236
Length of hind foot	−0.952	−0.009	0.158	−0.899	−0.109	−0.145
Greatest length of skull	−0.974	−0.080	−0.016	−0.975	−0.124	0.006
Zygomatic breadth	−0.947	−0.073	−0.154	−0.891	−0.121	0.227
Interorbital constriction	−0.883	−0.145	−0.164	−0.836	−0.208	0.161
Mastoid breadth	−0.844	−0.181	−0.291	−0.877	−0.121	0.229
Length of nasals	−0.961	0.059	−0.006	−0.951	0.058	0.060
Length of rostrum	−0.967	−0.003	0.020	−0.971	−0.038	−0.120
Length of maxillary toothrow	−0.504	−0.579	−0.335	−0.550	−0.559	−0.484
Depth of braincase	−0.856	−0.198	0.252	−0.871	−0.152	−0.037
Interparietal width	−0.692	−0.433	0.014	−0.501	−0.121	0.784
Interparietal length	−0.819	0.266	0.128	−0.835	0.279	0.171
Posterior margin of interparietal	−0.487	0.697	−0.280	−0.621	0.564	−0.184
Division of interparietal	0.490	−0.733	−0.255	0.490	−0.748	0.104
Posterior margin of nasals	−0.325	0.613	−0.599	−0.260	0.594	−0.081
Length of premaxillary bones	0.256	−0.709	−0.219	0.271	−0.748	−0.018



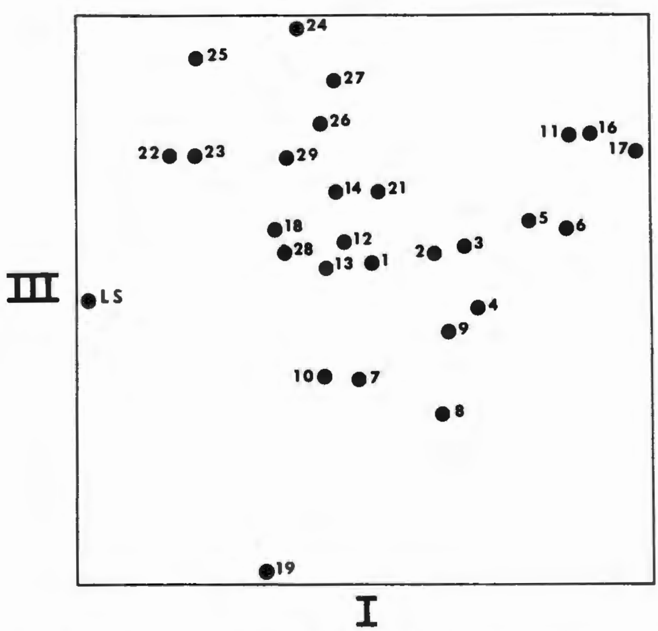


FIG. 23.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 27 samples of male *Liomys pictus* and one of *Liomys spectabilis* (LS). Top, component I plotted against component II; bottom, component I plotted against component III. See Fig. 19 and text for key to samples.

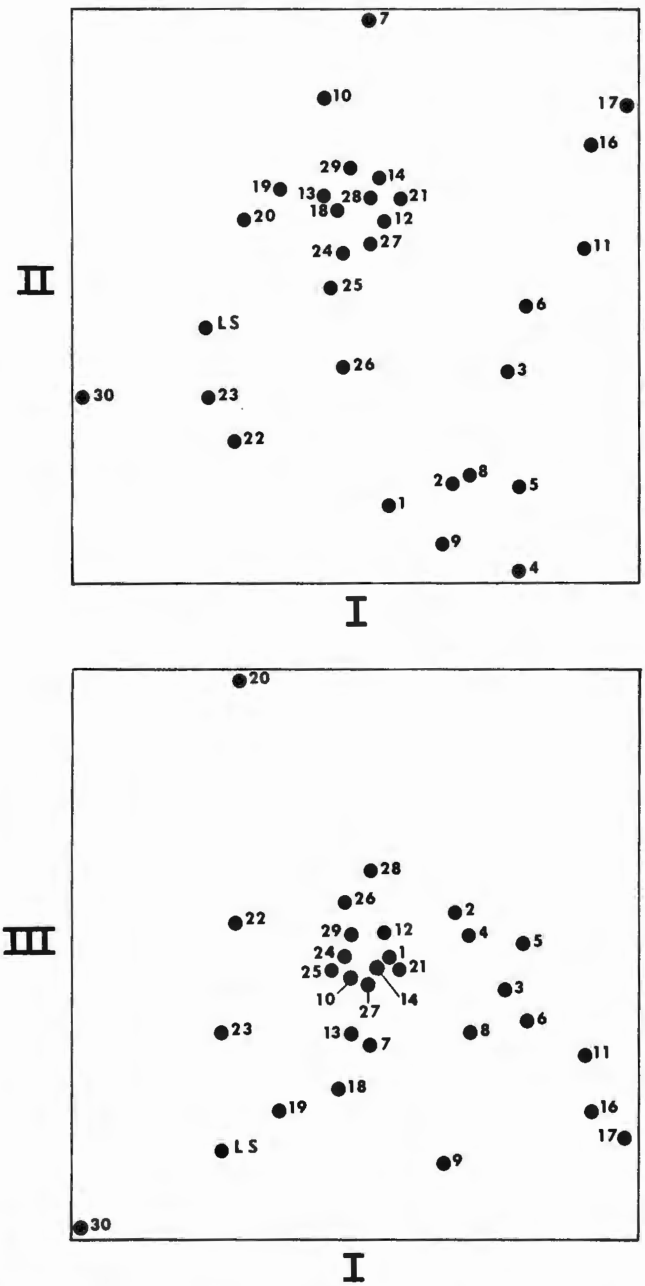


FIG. 24.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 29 samples of female *Liomys pictus* and one of *Liomys spectabilis* (LS). Top, component I plotted against component II; bottom, component I plotted against component III. See Fig. 19 and text for key to samples.

Another group includes samples 22, 23, and 25. Two samples (22, 23) included here are in the high mountains of Oaxaca and the other (sample 25) consists of specimens from southeastern Oaxaca and northwestern Chiapas and is not contiguous geographically with the other two samples; these three samples are made up of the largest males of the species. One possible explanation why males from sample 25 are larger than males from surrounding samples is that this is the area where *Liomys pictus* and *Liomys salvini* occupy sympatric ranges and some degree of character displacement may be involved (see section of specific relationships following the species accounts). The last group includes samples 6, 11, 16, and 17, although, as stated above, sample 6 is out of place here on geographic grounds. The remaining three samples form a contiguous series in interior Jalisco, Michoacán, and Guerrero that is characterized by uniformly small size.

The distance phenogram for female *Liomys pictus* reveals essentially the same four clusters seen in males, in addition to a fifth group composed only of sample 30. The first cluster for females is the same as that for males excepting that sample 6 is included with this group as might be expected on geographic grounds. The second cluster differs from that of males only in that sample 19 is farther away from the group and falls almost in an intermediate position between it and the next group. The third cluster of samples includes 20, 22, and 23, which are the three samples from the mountains of Oaxaca. The individuals in this group, except for the three specimens from sample 30, are the largest females of the species. The fourth cluster of samples for females includes only the three samples from interior Jalisco, Michoacán, and Guerrero (11, 16, 17) from which specimens are characterized by small size. Sample 30 appears to fall some "distance" from the other samples, but it should be remembered that there are only four specimens included in this sample.

In the principal components analysis, the amount of phenetic variation represented in the first three components for male and female *Liomys pictus,* respectively, was 61.23 and 60.48 per cent in component I, 15.40 and 13.84 in component II, and 5.97 and 7.08 in component III. Results of a factor analysis showing characters influencing the first three components is given in Table 15. From this analysis, it is apparent that the first, and by far the most important, component is heavily influenced by general size. The second component for both sexes is influenced by the qualitative cranial characters. Characters influencing the third component appear to be different between the sexes; for males, there is high positive weighting for length of tail and depth of braincase and high negative values for length of maxillary toothrow and the qualitative cranial characters, whereas for females interparietal width has a high positive value and length of maxillary toothrow has a high negative value. Examination of the two-dimensional plots (I-II and I-III, see Figs. 23, 24) and the three-dimensional projections (Figs. 25, 26) of the samples reveals a pattern similar to that shown in the distance phenogram. Samples 1 to 6 for males form a chain of samples that represents the clinal variation seen in many of the characteristics in the univariate analysis. Specimens from sample 1 fall at the lower end of the phenetic variation of specimens in group 2 (see below), but the geographic position of this sample

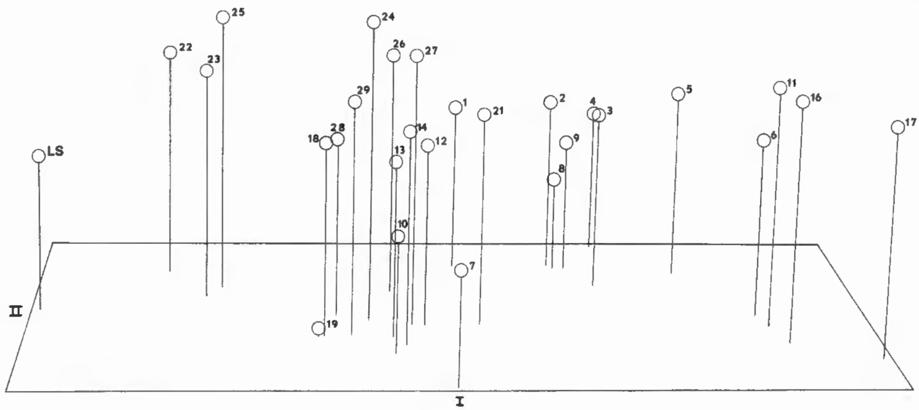


FIG. 25.—Three-dimensional projection of 27 samples of male *Liomys pictus* and one of *Liomys spectabilis* (LS) onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 19 and text for key to samples.

(Sonora and northern Sinaloa) makes such an arrangement taxonomically unacceptable. Specimens from sample 6 at the small end of this cline have a phenetic position near other samples of small specimens from interior Jalisco, Michoacán, and Guerrero, but again on geographical grounds this is an unacceptable arrangement. Specimens from samples 8 and 9 also fall into this group, but at a position that is nearly intermediate between the small individuals to the north (6) and the large individuals to the west (7 and 10). The second group for males is composed of samples 7, 10, 12 to 14, 18, 19, 21, 24, and 26 to 29. Sample 21 falls relatively far from its contiguous populations but appears to be phenetically most aligned with this group. A third group of samples is composed of 22, 23, and 25. Sample 25 is discontinuous from the other two, which are from the mountains of Oaxaca, and probably is best thought of as an extreme phenetic variate of the second group (above). The fourth cluster in the analysis of males is made up of the samples from the interior of Jalisco, Michoacán, and Guerrero (11, 16, 17). Sample 6 fits here phenetically but this would not be acceptable geographically as seen above. Females exhibit nearly the same phenetic patterns as males. Sample 6 is placed phenetically closer to its geographically contiguous populations in northwestern México and would appear to fit well at the end of this cline. Specimens from sample 25 are placed with the second group of samples as their geographic location would suggest. Females from sample 19 have a phenetic position that lies between the second and third group of samples and possibly represent a transition between the groups. Sample 30 is rather far removed from any other sample but is nearest the group of 20, 22, and 23.

Variation in Color

The results of my studies of variation in color should be considered as only preliminary, for the reasons enumerated in the section on methods and mate-

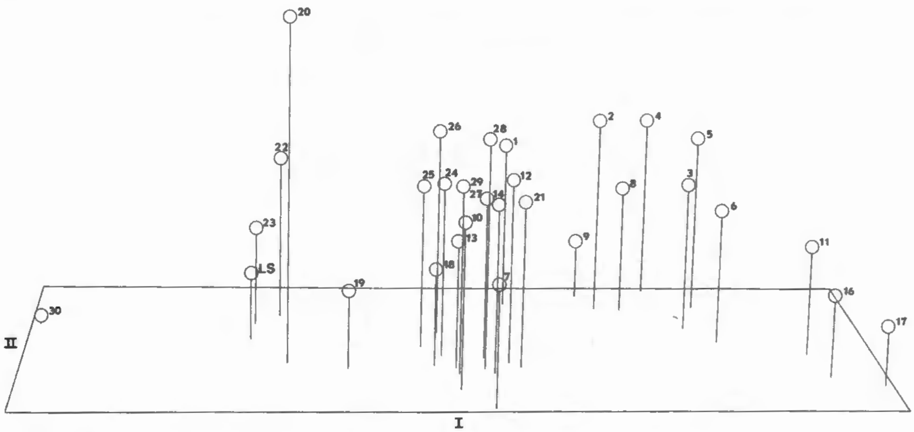


FIG. 26.—Three-dimensional projection of the 29 samples of female *Liomys pictus* and one of *Liomys spectalis* (LS) onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 19 and text for key to samples.

rials, but they do show some trends in variation (Table 16). Specimens from high elevations are uniformly darker than specimens from adjacent lowlands (see Fig. 27). One striking example of the change in color from montane areas to lowlands is seen along the southern coast of Oaxaca. Specimens from south of Candelaria (4 mi. S Candelaria is the farthest south) are dark but specimens from about 5 kilometers to the south at Chacalapa are pale and resemble other lowland mice. A similar situation is seen when specimens from the vicinity of San Gabriel Mixtepec (dark) are compared with two specimens from Cycad Camp (pale). In this latter case, according to notes by field collectors, the dark mice were found in pine-oak forest, whereas the pale mice were trapped in tropical arid scrub forest.

Two other localities from which dark specimens have been collected of which special note should be made are Finca San Salvador (29) and San Andrés Tuxtla (32). Finca San Salvador is in the coastal mountains of Chiapas near the type locality of *Liomys pinetorum*, which was described as a dark species. San Andrés Tuxtla is located on the Sierra Los Tuxtlas—an isolated group of mountains on the coast of Veracruz.

Particularly pale specimens were from dry areas such as the Sonoran desert (1), along the Balsas River (18), and lowlands of the Isthmus of Tehuantepec (24). Specimens from the highest areas of the Isthmus (25) are darker than those from coastal lowlands but not as dark as specimens from higher elevations. In only one case are lowland specimens darker than those from the adjacent highland; this involves specimens from the vicinity of San Blas, Nayarit, as compared with those from the vicinity of Tepic and Compostela, Nayarit.

I feel, as did Hooper (1955:9), that color in and of itself is not a sufficient indicator of major patterns of geographic variation, but that it reflects variation with altitude and the ecological situations in which specimens were obtained. In

TABLE 16.—*Geographic variation in dorsal coloration of 35 samples of* Liomys pictus. *Samples differ from those used for univariate and multivariate analyses. See discussion of coloration of* Liomys irroratus.

Sample	N	Red			Green			Blue		
		Mean ± 2 SE	Range	CV	Mean ± 2 SE	Range	CV	Mean ± 2 SE	Range	CV
1 (Sonora:Alamos)	10	15.3 ± 0.88	(13.5-18.0)	9.2	8.2 ± 0.61	(7.0-10.0)	11.9	7.3 ± 0.48	(6.5-8:5)	10.4
2 (Sinaloa:Cosalá, San Ignacio)	8	13.1 ± 0.70	(11.5-14.5)	7.6	7.3 ± 0.71	(6.0-8.5)	13.8	6.5 ± 0.60	(5.0-7.5)	13.0
3 (Sinaloa:Santa Lucía)	10	11.3 ± 0.70	(10.0-13.0)	9.8	6.0 ± 0.50	(5.0-7.0)	13.4	5.5 ± 0.36	(5.0-6.5)	10.5
4 (southern Sinaloa)	30	13.4 ± 0.67	(9.5-17.0)	13.7	6.8 ± 0.39	(5.0-9.0)	15.8	6.2 ± 0.37	(4.5-9.0)	16.3
5 (Nayarit:Platanares, Rosa Morada)	14	13.5 ± 0.52	(12.0-15.5)	7.2	7.5 ± 0.28	(7.0-8.5)	6.9	7.0 ± 0.32	(6.5-8.5)	8.6
6 (Nayarit:Aticama, Las Varas, San Blas)	9	12.2 ± 0.97	(10.5-14.5)	12.0	6.6 ± 0.31	(6.0-7.0)	7.1	6.1 ± 0.32	(5.5-7.0)	8.0
7 (Nayarit:Compostela, Ixtlan del Río, Tepic)	13	14.5 ± 0.62	(12.0-16.0)	7.8	8.0 ± 0.26	(7.0-8.5)	6.0	7.3 ± 0.21	(6.5-8.0)	5.1
8 (Nayarit:Amatlán de Cañas Jalisco:Amatitán, Guadalajara, Tequila)	13	13.1 ± 0.62	(11.5-15.0)	8.5	7.8 ± 0.55	(6.5-9.5)	12.6	7.4 ± 0.43	(6.5-9.0)	10.5

TABLE 16.—*Continued.*

9 (Jalisco:Puerto Vallarta)	5	13.8 ± 1.89	(10.5-15.5)	15.3	6.9 ± 0.80	(5.5-7.5)	13.0	6.3 ± 1.08	(5.0-7.5)	19.1
10 (Jalisco:Milpillas, San Sebastián)	8	12.3 ± 0.46	(11.5-13.5)	5.3	6.4 ± 0.40	(6.0-7.5)	8.7	5.5 ± 0.50	(5.0-7.0)	12.7
11 (southwestern Jalisco)	10	13.7 ± 0.90	(11.0-15.5)	10.4	6.4 ± 0.42	(5.0-7.0)	10.3	5.9 ± 0.40	(5.0-7.0)	10.7
12 (Jalisco:Contla)	20	14.6 ± 0.48	(12.0-16.5)	7.4	7.9 ± 0.31	(6.5-9.5)	8.8	7.1 ± 0.31	(6.0-8.0)	9.8
13 (Michoacán: Apatzingán)	5	15.2 ± 1.50	(14.0-18.0)	11.1	8.3 ± 0.40	(8.0-9.0)	5.4	7.6 ± 0.49	(7.0-8.5)	7.2
14 (Michoacán:La Mira)	1	14.5			7.5			7.0		
15 (Guerrero:Acapulco)	10	12.1 ± 1.29	(9.5-17.0)	16.8	6.6 ± 0.65	(5.5-9.0)	15.5	6.3 ± 0.73	(5.0-9.0)	18.6
16 (Guerrero:Agua del Obispo)	12	10.6 ± 0.94	(7.0-13.0)	15.5	5.5 ± 0.49	(3.5-6.5)	15.5	4.9 ± 0.37	(3.5-6.0)	13.2
17 (Guerrero:Omilteme)	5	10.8 ± 0.87	(9.5-12.0)	9.0	5.5 ± 0.71	(4.5-6.5)	14.4	5.4 ± 0.80	(4.0-6.5)	16.6
18 (Guerrero:Los Sabinos, Río Balsas)	13	15.2 ± 0.73	(13.5-17.5)	8.7	7.7 ± 0.56	(6.5-10.0)	13.2	6.7 ± 0.43	(5.5-8.5)	11.6
19 (Oaxaca:La Concepción, San Vincente)	3	10.8 ± 0.88	(10.0-11.5)	7.1	5.5 ± 0.58	(5.0-6.0)	9.1	5.0 ± 1.13	(4.0-6.0)	20.0
20 (Oaxaca:Juchatengo, San Gabriel Mixtepec, Sola de Vega)	24	11.8 ± 0.67	(8.5-14.5)	14.0	6.2 ± 0.38	(4.5-8.0)	15.0	5.9 ± 0.34	(4.0-7.0)	13.9
21 (Oaxaca:Candelaria, Pluma)	13	10.7 ± 0.55	(9.5-12.5)	9.3	5.5 ± 0.30	(5.0-6.5)	9.8	5.2 ± 0.21	(4.5-6.0)	7.4
22 (Oaxaca:Chacalapa)	12	15.1 ± 0.83	(13.0-18.5)	9.5	7.8 ± 0.31	(7.0-9.0)	7.0	6.8 ± 0.28	(6.0-7.5)	7.2
23 (Oaxaca:Puerto Angel)	13	14.1 ± 0.56	(12.5-16.0)	7.1	7.3 ± 0.31	(6.5-8.0)	7.6	6.8 ± 0.27	(6.0-7.5)	7.1

TABLE 16.—*Continued.*

24 (Oaxaca:Escurano, Salazar, Santa Lucía, Tehuantepec)	25	15.7 ± 1.02	(12.0-21.5)	16.3	7.8 ± 0.59	(6.0-10.5)	19.0	7.0 ± 0.50	(5.0-9.5)	17.9
25 (Oaxaca:Guichicovi, Mixes, Santo Domingo)	10	12.3 ± 0.80	(10.0-14.0)	10.4	6.0 ± 0.49	(5.0-7.5)	13.0	5.4 ± 0.33	(4.5-6.0)	9.9
26 (Oaxaca:Santa Efigenia)	10	13.8 ± 0.45	(12.5-15.0)	5.2	6.5 ± 0.28	(6.0-7.0)	6.8	5.7 ± 0.27	(5.0-6.5)	7.4
27 (Chiapas:Tonalá)	8	13.0 ± 1.20	(10.5-14.0)	13.0	6.8 ± 0.63	(5.5-8.0)	13.1	6.0 ± 0.53	(5.5-7.0)	12.6
28 (Chiapas:Tuxtla Gutiérrez, valley of Jiquipilas)	9	13.9 ± 0.78	(12.0-16.0)	8.4	6.7 ± 0.50	(5.5-8.0)	11.2	6.1 ± 0.36	(5.5-7.5)	8.9
29 (Chiapas:Finca San Salvador)	6	11.5 ± 0.86	(10.5-13.5)	9.1	6.3 ± 0.56	(5.5-7.5)	11.0	5.8 ± 0.56	(5.0-7.0)	12.0
30 (Chiapas:La Trinitaria)	5	12.2 ± 1.12	(11.0-13.5)	10.3	6.9 ± 0.73	(6.0-8.0)	11.9	6.2 ± 0.81	(5.0-7.5)	14.7
31 (Veracruz:Pasa Nueva)	6	14.1 ± 1.11	(12.5-16.5)	9.6	6.5 ± 0.26	(6.0-7.0)	4.9	6.1 ± 0.31	(5.5-6.5)	6.2
32 (Veracruz:Catemaco, San Andrés Tuxtla)	8	11.3 ± 0.91	(9.5-13.5)	11.4	5.4 ± 0.49	(4.5-6.5)	12.9	5.3 ± 0.46	(4.5-6.0)	12.5
33 (Veracruz:Alvarado)	6	16.3 ± 0.61	(15.0-17.0)	4.6	8.5 ± 0.45	(7.5-9.0)	6.4	7.7 ± 0.42	(7.0-8.5)	6.7
34 (Veracruz:Boca del Río, Puente Nacional)	7	13.4 ± 1.32	(11.0-16.0)	13.1	6.7 ± 0.65	(5.5-8.0)	12.8	5.9 ± 0.59	(5.0-7.0)	13.3
35 (Veracruz:Paraje Nuevo, San Juan de la Punta)	3	12.2 ± 1.76	(10.5-13.5)	12.6	6.0 ± 1.00	(5.0-6.5)	14.4	5.0 ± 0.58	(4.5-5.5)	10.0

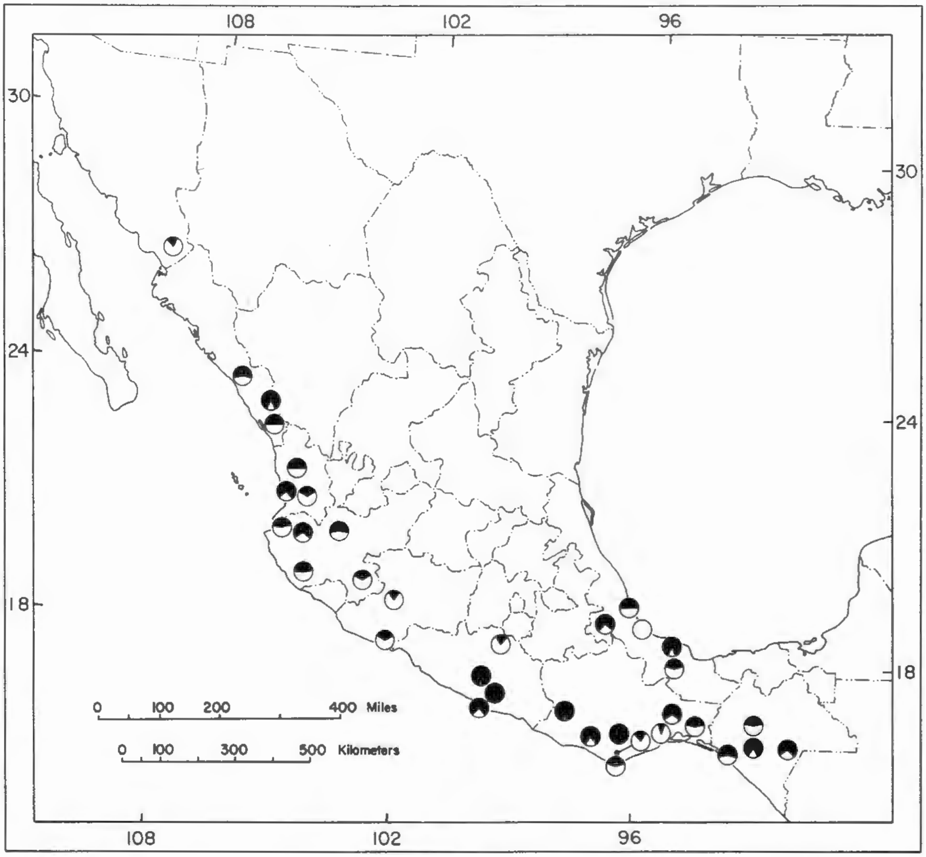


FIG. 27.—Geographic variation in red reflectance of middorsal coloration of *Liomys pictus*. The palest sample is represented by an open symbol, the darkest sample by a completely closed symbol, and the remaining samples by symbols that are expressed as a percentage of the difference between these extremes. See Table 16 for areas represented by symbols.

only one case (disscussed below) do I believe that color may be a useful indicator of geographic variation and in this situation it is correlated with many other characteristics.

Taxonomic Conclusions

Based upon my study of the geographic variation of *Liomys pictus,* I have chosen to recognize four subspecies. The first occupies the coastal areas and adjacent highlands of Sonora, Sinaloa, Durango, Chihuahua, and northern Nayarit. In southern Nayarit this subspecies is confined to the higher interior regions around Tepic and continues southeastward to the vicinity of Guadalajara, Jalisco. The oldest available name for this race is *Liomys pictus hispidus* (J. A. Allen, 1897) with type locality at Compostela, Nayarit. The second subspecies reaches the northern limit of its range in the vicinity of San Blas, Nayarit. From San Blas it extends southward along the coast and Pacific slope of the Sierra Madre del Sur of Jalisco and Colima and along the coasts of Michoacán, Guerrero, and Oaxaca into the Isthmus of Tehuantepec; hence it ranges to northwestern Chiapas and the central valley of Chiapas, and into the lowlands of southern Veracruz. The oldest available name for this group is *Liomys pictus pictus* (Thomas, 1893) with type locality of San Sebastián, Jalisco. The third subspecies that I recognize occupies a range that includes the interior drainage basins of Jalisco and Michoacán, and along the Río Telalcatepec, Michoacán, and Río Balsas, Guerrero, and their tributaries. The name for this group is *Liomys pictus plantinarensis* Merriam, 1902, with holotype from Platanar, Jalisco. The fourth subspecies, *Liomys pictus annectens* (Merriam, 1902) previously was considered a full species. The geographic range of this race is restricted to the high mountains of the Sierra Madre del Sur of Guerrero and Oaxaca, with holotype from Pluma Hidalgo, Oaxaca. The distribution and relationship of these four subspecies will be discussed at length in the accounts that follow.

Liomys pictus annectens (Merriam, 1902)

1902. *Heteromys annectens* Merriam, Proc. Biol. Soc. Washington, 15:43, 5 March.
1911. *Liomys annectens*, Goldman, N. Amer. Fauna, 34:45, 7 September.

Holotype.—Adult male, skin and skull, USNM 71510, from Pluma Hidalgo, Oaxaca; obtained on 18 March 1895 by E. W. Nelson and E. A. Goldman. Skin and skull in good condition.

Measurements of holotype.—Total length, 300; length of tail, 165; length of hind foot, 33; greatest length of skull, 34.3; zygomatic breadth, 16.1; interorbital constriction, 7.9; mastoid breadth, 14.7; length of nasals, 14.7; length of maxillary toothrow, 5.3; depth of braincase, 8.9; interparietal width, 8.8; interparietal length, 4.1.

Distribution.—Confined to high elevations (lowest elevation from which specimens are known is approximately 2500 feet) in the Sierra Madre del Sur of Guerrero and Oaxaca from Omilteme, Guerrero, to Sierra de San Felipe Lachilló, Oaxaca (Fig. 28). Intergrading with *Liomys pictus pictus* at lower elevations along the Pacific slope of the Sierra Madre.

Comparisons.—From *Liomys pictus pictus,* the subspecies *annectens* differs as follows: larger both externally and cranially (compare values for samples 22, 23 with those for 18, 21, 24 in Table 11), color noticeably darker dorsally, and lateral stripe darker orange and more clearly distinct from the dorsal coloration. The only qualitative cranial character in which these two subspecies differ is that the premaxillary and nasal bones terminate at the same level in a slightly greater percentage of individuals of *annectens* than in contiguous populations of *pictus* (Table 14).

Liomys pictus annectens differs from *Liomys pictus hispidus* as follows: larger both externally and cranially (compare values for samples 22, 23 with those of 1-6 in Table 11), color noticeably darker dorsally, and lateral stripe darker orange and more clearly distinct from the dorsal coloration. Only one individual

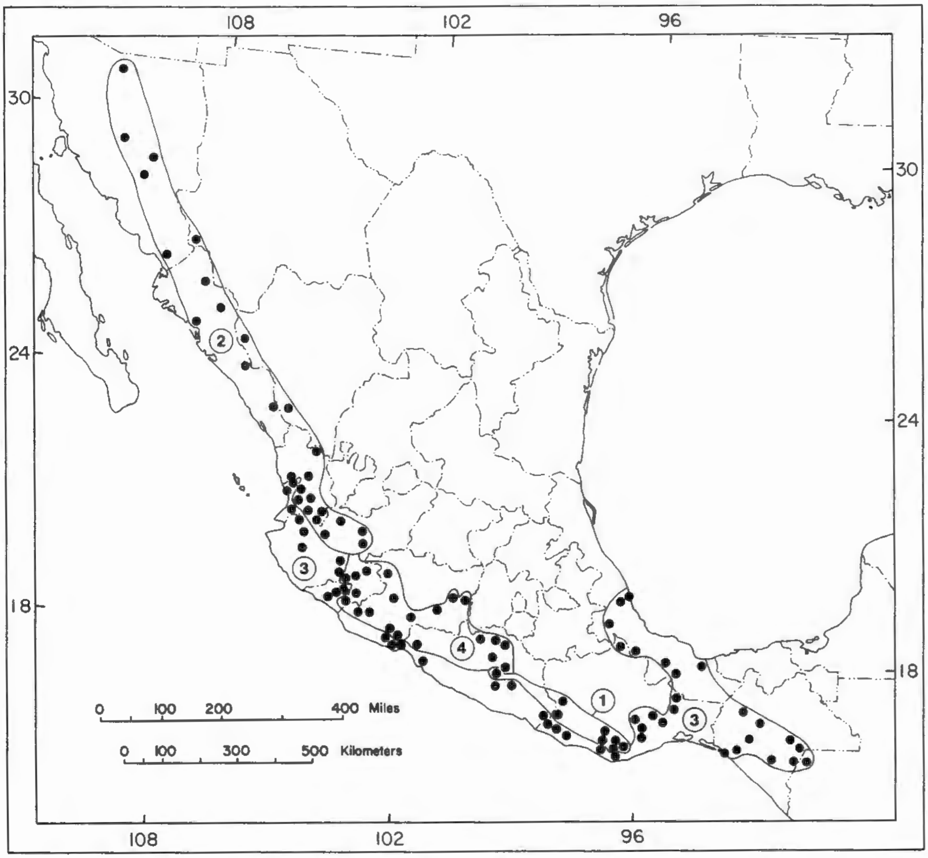


FIG. 28.—Geographic distribution of subspecies of *Liomys pictus*: 1, *L. p. annectens*; 2, *L. p. hispidus*; 3, *L. p. pictus*; 4, *L. p. plantinarensis*.

of *annectens* had a divided interparietal bone, whereas the bone was divided in more than 50 per cent of the individuals of *hispidus* examined (Table 13).

Comparison of *annectens* with *Liomys pictus plantinarensis* is given in the account of that subspecies.

Remarks.—Until the present study, this taxon was considered a species distinct from *Liomys pictus*; however, there is sufficient evidence for intergradation between the two taxa from at least one place along the lower slope of the Sierra Madre del Sur in southern Oaxaca to regard *annectens* as a subspecies of *pictus*. Discriminant function analysis was conducted on 10 cranial measurements using the MULDIS program between groups from the coastal lowlands of Oaxaca and Guerrero regarded as typical of *pictus* and mice from the highlands around San Gabriel Mixtepec and Juchatengo, Oaxaca, that are typical of *annectens*. Table 17 gives the discriminant multipliers generated by this analysis. When the discriminant scores are plotted as a histogram (Fig. 29), it can be seen that two groups (generally corresponding to the original two reference samples) are formed.

TABLE 17.—*Discriminant multipliers resulting from a discriminant function analysis comparing* Liomys pictus pictus *from coastal Oaxaca and Guerrero and* Liomys pictus annectens *from coastal mountains of Oaxaca.*

Character	Discriminant multiplier
Length of hind foot	0.182
Greatest length of skull	−0.528
Interorbital constriction	−0.035
Mastoid breadth	−0.653
Length of nasals	1.160
Length of rostrum	0.533
Length of maxillary toothrow	3.391
Depth of braincase	1.180
Interparietal width	0.608
Interparietal length	0.219

However, a few individuals of both reference groups occupy the middle of the histogram at a position indicating that, on the basis of the 10 cranial characters used, these individuals could not be placed into one group or the other. No overlap in discriminant scores was observed when species recognized in this paper were analyzed.

Next, cranial measurements of individuals from an altitudinal transect along the Pacific slope of the Sierra Madre del Sur were multiplied by the proper discriminant multipliers and the resulting discriminant scores plotted on the histogram (Fig. 29). Specimens from Pluma Hidalgo (marked PL on Fig. 29), which is at the highest elevation on the transect (between 3000 and 4000 feet according to Goldman, 1951:219) and the type locality of *annectens,* all were within the range of values for the *annectens* reference sample. The next localities were at 3 mi. S and 4 mi. S Candelaria (marked CA on Fig. 29) at approximately 2500 feet elevation. The five adults from these localities exhibited a wide range of variation; two specimens were within the range of values for the *annectens* reference sample, two specimens fall near the middle of the histogram where it was difficult to assign them to either group, and one specimen was within the range of values for the *pictus* reference sample. The locality at the lowest elevation on this transect was Chacalapa (marked CH on Fig. 29) at approximately 1500 feet. All of the specimens from Chacalapa were within the range of values for the *pictus* reference sample. I have interpreted these results to mean, firstly, that the two groups are not as distinct as species of *Liomys* that I have tested during this study and, secondly, intergradation is indicated between the two taxa in the vicinity of Candelaria. The specimens from Candelaria all have retained the dark coloration of *annectens,* to which I have assigned them subspecifically.

The point of contact between *pictus* and *annectens* seems to correspond roughly to vegetation types in the area. Goldman (1951:219), describing the area

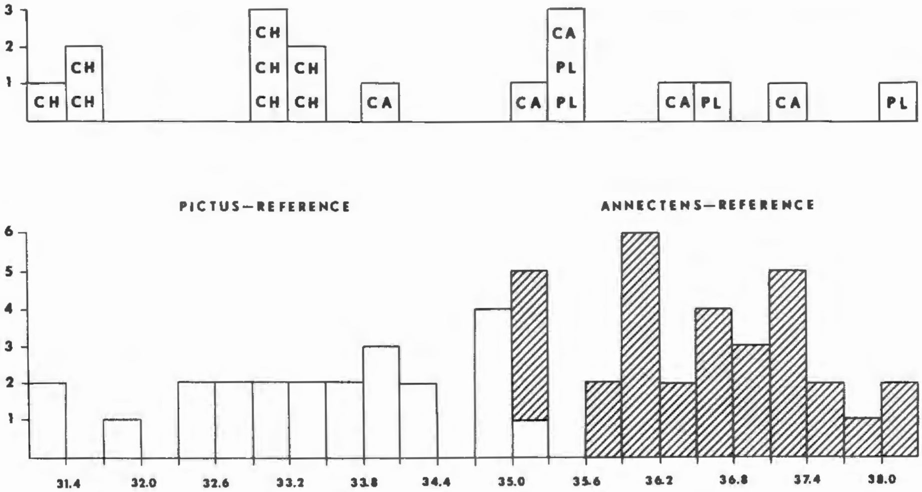


FIG. 29.—Histogram of linear discriminant scores based on a discriminant function analysis comparing *Liomys pictus pictus* from coastal Oaxaca and Guerrero and *Liomys pictus annectens* from the mountains of southern Oaxaca. Discriminant scores are indicated along the bottom of the histogram and frequency of individuals is indicated on the left-hand side. Individuals arranged below are from reference samples of *pictus*, at left, and *annectens*, at right. Individuals arranged above are from the test sample, which is from the vicinities of the following localities in Oaxaca: PL, Pluma Hidalgo; CA, Candelaria; CH, Chacalapa.

in the vicinity of Pluma Hidalgo, stated: "The Arid Lower Tropical coast belt ends at about 2,500 feet on the mountain facing the sea. A Humid Upper Tropical area extends from 2,500 feet up to about 5,000 feet. . . ." The break between those two vegetational types is at approximately the same elevation as the zone of intergradation between the two subspecies south of Candelaria. A similar situation is seen when specimens from the vicinity of San Gabriel Mixtepec are examined; here, mice from San Gabriel and northward are dark and large and referable to *annectens*, whereas those from a lower elevation, Cycad Camp, are smaller and paler and are referable to *pictus*. According to the notes of field collectors, dark-colored mice were trapped in pine-oak forest, whereas the pale mice were taken in tropical arid scrub forest.

On the basis of the data given above, I consider *annectens* as a member of the species *pictus* that is distinguished from other subspecies by its large external and cranial size and dark coloration. The only qualitative cranial characteristic that appears even slightly different from contiguous populations of *pictus* is that a slightly greater percentage of *annectens* have the nasals terminating at the same level as the premaxillaries.

The specimens from Omilteme, Guerrero, were fairly widely separated from the Oaxacan samples of *annectens* in the univariate and multivariate analyses, although they were closer to individuals from these samples than to any others. Because the sample from Omilteme contained only four adult females, I have placed them with *annectens* pending acquisition of material that more definitely indicates the relationships of mice from this area.

I have examined specimens from two localities in Sierra Madre del Sur—La Cima and Río Molino—of Oaxaca from which individuals of both *Liomys pictus annectens* and *Liomys irroratus irroratus* were collected. Unfortunately, no notes are available on the ecological distribution of these two species in this situation, which is much moister than any other from which both species are known. At Omilteme, Guerrero, *annectens* occurs in the same general area as *Liomys irroratus guerrerensis,* but again no data is available on the precise habitats occupied.

Six adult males and 10 nonpregnant, adult females from southern Oaxaca weighed, respectively, 61.1 (56.7-64.5) and 48.6 (41.1-55.8) and had ears that measured 16.8 (16.0-18.0) and 15.8 (14.0-17.5).

Specimens examined (147).—GUERRERO: 1 mi. NW Omilteme, 7260 ft., 2 (USNM); 2 mi. W Omilteme, 7900 ft., 3 (TCWC); 1 mi. W Omilteme, 2 (UMMZ); Omilteme, 6 (USNM).

OAXACA: 3 mi. S Candelaria, 8 (KU); 4 mi. S Candelaria, 4 (KU); Finca Sinai, 10 km. E Nopala, 7200 ft., 15 (CAS); Jamaica Junction, km. 212 on Oaxaca-Puerto Escondido Road, 18 (CAS); 10 mi. S Juchatengo, 5350 ft., 9 (KU); La Concepción, 1 (AMNH); Mesones, 1 (AMNH); km. 136 on Oaxaca-Puerto Escondido Road, 3500 ft., 6 (CAS); km. 183 on Oaxaca-Puerto Escondido Road, 6000 ft., 3 (CAS); km. 198 on Oaxaca-Puerto Escondido Road, 5 (CAS); km. 212½ on Oaxaca-Puerto Escondido Road, 2100 ft., 2 (CAS); km. 214 Oaxaca-Puerto Escondido Road, 6000 ft., 3 (CAS); km. 123 on Putla-Tlaxiaco Road, 4 (CAS); km. 135 on Putla-Tlaxiaco Road, 3250 ft., 1 (CAS); Pluma, 6 (USNM); Putla, 1 (AMNH); Río Guajolote, 2000 m., 2 (UNAM); Río Molino, 2250 m., 1 (UNAM); 23 mi. (Hwy. 131) N San Gabriel Mixtepec, 1700 m., 1 (UMMZ); 2 mi. E San Gabriel Mixtepec, 12 (AMNH); ½ mi. SE San Gabriel Mixtepec, 9 (AMNH); San Juan Lachao, 2 (AMNH); 12 km. S San Juan Lachao, 1350 m., 2 (ENCB); San Vincente, 4 (AMNH); Sierra de San Felipe Lachilló, 1 (AMNH); 20 mi. S, 5 mi. E Sola de Vega, 4800 ft., 11 (KU); Zacatepec, 1 (AMNH).

Marginal records.—GUERRERO: 1 mi. NW Omilteme. OAXACA: San Vincente; km. 136 on Oaxaca-Puerto Escondido Road; Río Molino; Sierra de San Felipe Lachilló; Pluma Hidalgo; *4 mi. S Candelaria;* ½ mi. SE San Gabriel Mixtepec; Zacatepec.

Liomys pictus hispidus (J. A. Allen, 1897)

1897. *Heteromys hispidus* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 9:56, 15 March.

1902. *Liomys sonorana* Merriam, Proc. Biol. Soc. Washington, 15:47, 5 March; holotype from Alamos, Sonora.

1906. *Heteromys pictus escuinapae* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 22:211, 25 July; holotype from Esquinapas [Escuinapa], Sinaloa.

Holotype.—Subadult female, skin and skull, AMNH 8333/6667, from Rancho El Colomo, Compostela, Nayarit; obtained on 11 February 1893 by A. C. Buller. Skin fairly well made, but lacking external measurements; skull in good condition.

Measurements of holotype.—Greatest length of skull, 30.5; interorbital constriction, 7.1; mastoid breadth, 13.9; length of nasals, 12.3; length of rostrum, 13.4; length of maxillary toothrow, 5.0; interparietal width, 8.8; interparietal length, 4.1.

Distribution.—Northwestern México, from 23 mi. S and 5 mi. E Nogales, Sonora, southward through coastal parts of Sinaloa and Nayarit and adjacent Pacific slopes of the Sierra Madre Occidental to the vicinity of San Blas, Nayarit

(Fig. 28). In southern Nayarit, *hispidus* is confined to the higher interior regions around Tepic and southeastward to the vicinity of Guadalajara, Jalisco, reaching the southern edge of its known geographic range at El Zapote, Jalisco. This subspecies is known also from three localities in extreme western Chihuahua and two in Durango.

Comparisons.—In the region of contact between the two subspecies, *Liomys pictus hispidus* differs from *Liomys pictus pictus* in having smaller external and cranial dimensions (compare values for samples 1-6 with those for 7, 10, 12-13 in Table 11). Specimens from the northern part of the geographic range of *hispidus* approach *pictus* in size, but those from the southern part of the range are much smaller than *pictus*. However, length of the interparietal bone is one characteristic in which populations of *hispidus* average uniformly shorter than contiguous populations of *pictus* (3.7-4.1 as opposed to 4.4-4.7) from Nayarit, Jalisco, and Colima. When qualitative cranial characters of the two subspecies are compared, *hispidus* is found to differ from *pictus* in having a high percentage of individuals with the interparietal bone divided (usually more than 50 per cent in most populations of *hispidus* as compared with only one individual observed with a divided interparietal in all populations of *pictus* that were studied—see Table 13); a tendency for individuals to have the posterior margin of the interparietal bone with a notch (more than 65 per cent of individuals with notch in populations of *hispidus* as compared with less than 40 per cent in northern populations of *pictus*—see Table 13); a high percentage of individuals with the premaxillary and nasal bones terminating at same level, especially in southern populations of *hispidus*; and in the region of contact (samples 4-6 as compared with 7, 10 in Table 14) a much higher percentage of individuals with nasal bones that are emarginate posteriorly. The specimens of *pictus* from the vicinity of San Blas, Nayarit, and other southwestern coastal areas of Nayarit are much darker than adjacent populations of *hispidus* but this is not true for most populations.

Comparisons of *Liomys pictus hispidus* with *Liomys pictus annectens* and *Liomys pictus plantinarensis* are given in the accounts of those subspecies.

Remarks.—The subspecific name *Liomys pictus hispidus* herein is applied to a series of populations occurring along the northwestern coast of México (samples 1-6) that varies in a clinal fashion from medium-sized individuals in Sonora and northern Sinaloa to relatively small individuals in northern Nayarit. In nearly all external and cranial measurements studied and in the multivariate analysis of all measurements, the clinal nature of the variation in these populations was evident. They also are characterized by a high percentage of individuals having a distinctive set of qualitative cranial characters as follows: interparietal bone divided; interparietal bone relatively short (as compared with *pictus*); nasal and premaxillary bones terminating at the same level; and nasal bones having an emarginate termination.

In the vicinity of San Blas, Nayarit, *hispidus* intergrades with *pictus* from coastal areas to the south. Two adult males from 11 mi. E San Blas (MSU 5745-46) have large external and cranial measurements (total length 233.0 and 245.0; greatest length of skull 31.9 and 33.1); long interparietal bones (4.8 and

4.7); nasals that are shorter than the premaxillaries and truncate posteriorly, and interparietals that are unnotched and undivided. All of these are characteristics of *pictus* and these specimens have been so assigned. A specimen from slightly farther east at Navarrete, Nayarit (USNM 88216), which has a broken skull, is large externally and cranially (total length, 229; length of rostrum, 14.7) and has a long interparietal bone (4.7). All these characteristics are typical of *pictus* to which race the specimen is assigned, but it has nasals that are emarginate posteriorly, definitely a characteristic of *hispidus* in this area. A subadult female from 17 mi. E San Blas (UNAM 3307) and an adult and subadult female from 29 km. E San Blas (UNAM 5758, 5762), on the other hand, show characteristics that are typical of *hispidus*—medium external and cranial size (greatest length of skull 30.6 in adult), short interparietal bone (3.5, 4.1, and 3.4), nasal and premaxillary bones of all three specimens terminating at the same level and nasals emarginate posteriorly, interparietal bone of one specimen divided and interparietals notched along posterior margin in all three specimens—and they are so assigned herein. Two subadult females from Santiago (USNM 91340 and 91365) are small externally and cranially (total length 216 and 210; greatest length of skull 29.0 and 28.9), but otherwise show characteristics of *pictus*—long interparietal bone (4.4 and 4.4); nasals shorter than premaxillaries; nasals rounded posteriorly in one specimen and truncate in the other; interparietal undivided and unnotched in both specimens. Subspecific assignment for these two specimens is at best questionable and definite allocation must await additional material from this area; however, for the present, I have relied on characters not related to age and placed them in *pictus*. Specimens from about 8 mi. E Santiago (at a place 17 km. SE Tuxpan) are some of the smallest specimens of *hispidus* that I have examined and show other characteristics that are typical of the subspecies.

Hooper (1955:9; 1957:3-4), commenting on the relationships of *Liomys pictus* from the vicinity of San Blas, pointed out that they resembled specimens from Jalisco and Colima more than specimens from eastern Nayarit and southern Sinaloa. He believed (1957:4) that the dark coloration of this population could be correlated with a humid tropical belt that extended from Bahía de Banderas, Nayarit, to the vicinity of Santiago and Navarrete with Compostela (type locality of *hispidus*) near its eastern edge and Santa Isabel, San José del Conde, and Ixtlán del Río to the east of it. The extent of this humid tropical belt would appear to outline closely the distribution of *Liomys pictus pictus* in Nayarit, although I believe, as will be shown below, that specimens from Compostela are best placed with the inland populations to the east.

Specimens from the vicinity of Tepic, Nayarit, and southeastward through Nayarit to just south of Guadalajara, Jalisco (samples 8 and 9), are intermediate in size between *pictus* to the west and *hispidus* to the north, as was seen in the univariate and multivariate analyses, but possess cranial characters that ally them with *hispidus*. I believe that specimens from Compostela (AMNH 8333/6667—holotype of *hispidus*) and 2 mi. S Compostela (KU 39837-39) are best placed with this group and for this reason the name *hispidus* has been applied to this population. It is an unfortunate circumstance that the type locality lies in a zone of intergradation between two widespread taxa, causing the resurrection of a name that has been carried in the synonymy of *pictus* since Goldman's revision in 1911. The relationship between these specimens and those from the adjacent coast (5 mi. S Las Varas and 8 mi. SSW Las Varas) are summarized in Table 18. Although specimens from the vicinity of Compostela are not "typical" *hispidus*, the preponderance of their characteristics ally them with the inland population more than with the coastal population, thereby leaving no choice but to apply the oldest available name—*hispidus*—to the inland mice. If one wishes to have "typical" specimens of *L. p. hispidus* to compare with other subspecies, material from the vicinity of Mazatlán, Sinaloa, would be appropriate, rather than specimens from the type locality.

Specimens from Ameca, Jalisco, were assigned to the subspecies *plantinarensis* by Goldman (1911:38); however, although I have not seen an adult from this area, I feel the specimens examined are best assigned to *hispidus*. Specimens from 7 mi. W Ameca (UMMZ 94724-25, 94729, and 94731) are only subadults, but their measurements are large enough to indicate relationship with *hispidus* (greatest length of skull for two males 31.9, 31.6 and two females 30.5 and 29.7; zygomatic breadth in same order 15.2, 15.3, 15.0, 14.7).

Specimens of *Liomys pictus hispidus* have been taken at the same locality as *Liomys irroratus jaliscensis* at six localities in Jalisco as follows: 3 mi. N Amatitán; 2 mi. NNW Amatitán; 1½ mi. WNW Amatitán; Ameca; 6 mi. W Ameca; and 7 mi. W Ameca. *Liomys irroratus* also was taken on the tableland just north of Guadalajara (3 mi. N and 3 mi. NW Guadalajara and 2 mi. N, ½ mi. W Guadalajara), whereas *Liomys pictus* has been taken in the more mesic habitats in the barranca of the Río Grande de Santiago (7-8 mi. N Guadalajara and 9 mi. NNE Guadalajara). Evidently, all localities where *pictus* has been taken in nothern Jalisco are near a mesic habitat and those areas where *pictus* and *irroratus* have been taken together are at the junction of mesic habitats and the drier uplands occupied by *irroratus*.

Mean length of ear for eight adult males and 10 adult females from the vicinity of Mazatlán, Sinaloa, was, respectively, 14.6 (12.0-17.0) and 13.4 (12.0-15.0); mean weight for these same animals was 50.7 (45.0-58.7) and 37.4 (32.9-40.3).

Specimens examined (978).—Chihuahua: near Batopilas [approximately 20 mi. W Batopilas according to Goldman, 1951:119], 2 (USNM); 40 km. N, 6 km. W Choix (Sinaloa), 2400 ft., 1 (KU); 40 km. N, 3 km. W Choix (Sinaloa), 2400 ft., 1 (KU).

Durango: Chacala, 10 (USNM); 2 mi. S Pueblo Nuevo, 3000 ft., 24 (MSU).

Jalisco: 3 mi. N Amatitán, 4050 ft., 1 (KU); 2 mi. NNW Amatitán, 4000 ft., 1 (KU); 1½ mi. WNW Amatitán, 4100 ft., 1 (KU); 7 mi. W Ameca, 4000 ft., 12 (UMMZ); 6 mi. W Ameca, 4300 ft., 1 (UMMZ); Ameca, 4 (USNM); Arroyo de Plantinar, 6 (AMNH); El Zapote, 2 (UNAM); Estancia, 10 (AMNH); 9 mi. NNE Guadalajara, 5 (KU); 8 mi. N Guadalajara, 3800 ft., 3 (KU); 7 mi. N Guadalajara, 3 (KU); Río Santa María, 8 (AMNH); 52 km. WNW Tequila, 2900 ft., 2 (CAS); 1 mi. N Tequila, 2 (KU); 2 mi. ESE Tequila, 4000 ft., 1 (KU).

Nayarit: Acaponeta, 21 (USNM); Amatlán, 7 (AMNH); 7 mi. ESE Amatlán de Cañas, 4750 ft., 5 (KU); 7 3/10 mi. ESE Amatlán de Cañas, 5000 ft., 5 (KU); 7½ mi. ESE Amatlán de Cañas, 5000 ft., 7 (KU); Compostela, Rancho El Colomo, 2 (AMNH); 2 mi. S Compostela, 2900 ft., 4 (KU); Huajicori, Río de Bajar, 20 (15 LACM, 5 UA); 3 mi. SE Huajicori, 5 (KU); 5 mi. SE Huajicori, 3 (KU); 1 mi. E Ixtlán del Río, 3700 ft., 35 (5 KU, 30 UMMZ);

TABLE 18.—*Selected cranial measurements and qualitative cranial characters of specimens of* Liomys pictus *from the zone of intergradation between the subspecies* hispidus *and* pictus *in southwestern Nayarit.*

Catalog number and sex	Greatest length of skull	Interparietal length	Nasal-premaxillary length	Nasal posterior	Interparietal posterior margin	Interparietal bone
			Compostela			
AMNH						
8333/6667 ♀	30.5	4.1	short	truncate	unnotched	undivided
			2 mi. S Compostela			
KU 39837 ♀	30.7	3.3	short	emarginate	notched	divided
KU 39838 ♀	31.5	3.9	just short	emarginate	notched	undivided
KU 39839 ♂	31.8	4.3	equal	emarginate	slight notch	undivided
			5 mi. S Las Varas			
KU 39824 ♀	32.0	4.8	short—10	truncate—8	unnotched—7	undivided—10
KU 39829 ♀	32.1	4.3	(all adults	rounded—1	slight notch—3	
			and subadults)	emarginate—1		
			8 mi. SSW Las Varas			
KU 64466 ♀	31.9	4.5	short	rounded	unnotched	undivided
KU 64467 ♂	31.7	4.7	short	truncate	unnotched	undivided
KU 64468 ♂	32.9	4.7	short	truncate	slight notch	undivided

½ mi. W Jalisco-Nayarit border on Mexican Hwy. 15, 1 (UA); La Cuchara, approximately 40 mi. E Acaponeta, 2 (LACM); Ojo de Agua, near Amatlán, 4 (AMNH); Pedro Pablo, 1 (USNM); Platanares, 10 mi. E Ruiz, 18 (KU); Playa Novilleros, 1 (UA); 3 km. S Playa Novilleros, 3 (UA); Rancho Palo Amarillo, near Amatlán, 11 (9 AMNH, 2 FMNH); 2 mi. SW Rosamorada, 13 (KU); 17 mi. E San Blas, 1 (UNAM); 29 km. E San Blas, 50 m., 14 (UNAM); 1 mi. SW San José del Conde, 3000 ft., 3 (UMMZ); 1½ km. N San Miguel, 1 (KU); 4 mi. N Santa Isabel, 3800 ft., 5 (UMMZ); 2 mi. N Santa Isabel, 3800 ft., 37 (UMMZ); 2 mi. WNW Tepic, 3200 ft., 7 (KU); Tepic, 9 (USNM); 20 mi. SE Tepic, 3500 ft., 2 (MSU); 17 km. SE Tuxpan, 480 ft., 10 (MSU).

SINALOA: 4 mi. NW Agua Nueva, 50 ft., 1 (MVZ); 20 km. N, 5 km. E Badiraguato, 1800 ft., 3 (KU); 1½ mi. N Badiraguato, 750 ft., 1 (KU); 1 mi. SE Camino Real, 400 ft., 1 (KU); Chele, 15 mi. N Rosario, 300 ft., 26 (25 UMMZ, 1 UNAM); 18 km. NNE Choix, 6 (KU); 16 km. NNE Choix, 1700 ft., 13 (KU); 1 mi. N Comanito, 1 (UNM); ½ mi. S Concepción, 250 ft., 16 (KU); 1½ mi. E Concordia, 250 ft., 6 (MSU); 3 mi. NE Copala, 2500 ft., 5 (MSU); 1 mi. N Copala, 3200 ft., 21 (MSU); Copala, 1600 ft., 30 (29 LACM, 1 MSU); 5 mi. SW Copala, 750 ft., 28 (MSU); Cosalá, 1300 ft., 2 (KU); 6 mi. E Cosalá, 1500 ft., 3 (KU); 2 mi. E Costa Rica, 100 ft., 2 (KU); 16 mi. NW Culiacán, 10 (UMMZ); 12 mi. N Culiacán, 400 ft., 2 (KU); Culiacán, 10 (USNM); 32 mi. SSE Culiacán, 2 (KU); 1 mi. S El Cajón, 1800 ft., 1 (KU); El Dorado, 1 (KU); 2 km. S El Dorado, 20 ft., 3 (KU); 6 km. NE El Fuerte, 150 m., 1 (KU); 3 mi. NE El Fuerte, 200 ft., 14 (KU); 6 km. E El Fuerte, 400 ft., 3 (KU); Elota, 1 (LACM); 2 mi. NW Escuinapa, 500 ft., 9 (KU); Escuinapa, 31 (26 AMNH, 5 MVZ); 15 mi. SE Escuinapa, 18 (UMMZ); 27 mi. SE Guamúchil on Mexican highway 15, 3 (UA); 24 km. S Guasave, 20 ft., 7 (KU); Hacienda San José, 21 mi. NE Rosario, 350 ft., 6 (MVZ); Isla Palmito de la Virgen, 15 ft., 6 (KU); Isla Palmito del Verde (middle), 1 (KU); Isla Palmito del Verde (S end), 2 (KU); km. marker 1206 on Mexican Hwy. 15, 2 (UA); 6 mi. W La Concha, 10 ft., 3 (KU); La Cruz, 30 ft., 4 (KU); Laguna, 17 km. SW Choix, 500 ft., 1 (KU); 7 3/10 km. SW Matatan, 500 ft., 20 (KU); 7½ km. SW Matatan, 500 ft., 1 (KU); 20 mi. N Mazatlán, 1 (UNAM); 9 mi. N Mazatlán, 9 (MSU); 10 km. N Mazatlán, 6 (UNAM); 5 mi. NW Mazatlán, 17 (KU); 4 mi. N Mazatlán, 2 (MSU); 3 mi. NNW Mazatlán, 25 ft., 1 (KU); 1 mi. N Mazatlán, 25 ft., 1 (MSU); Mazatlán, 2 (1 MCZ, 1 MSU); 5 mi. WSW Mazatlán, 3 (AMNH); near Mazatlán [approximately 9 mi. SE Mazatlán according to Goldman, 1951: 249], 15 (USNM); Pánuco, 22 km. NE Concordia, 5 (KU); 23 km. W Pericos, 200 ft., 2 (LACM); 1 mi. S Pericos, 1 (KU); Piaxtla, 100 ft., 1 (KU); Plomosas, 12 (1 KU, 11 USNM); 2 mi. SW Plomosas, 3050 ft., 4 (KU); 12 mi. NE Presa Sanalona, 600 ft., 3 (KU); 11 mi. ENE Presa Sanalona, 500 ft., 8 (KU); Puerta de Canoa, 11 mi. N, 2½ mi. E Mazatlán, 6 (LACM); W side Río Chametla, 1 mi. NE Rosario, 1 (MVZ); Rosario, 7 (1 MCZ, 6 USNM); 4 mi. SW Rosario, 7 (MVZ); 5 mi. SSE Rosario, 100 ft., 5 (KU); San Juan, 8 mi. SE San Ignacio, 3 (KU); San Ignacio, 700 ft., 1 (KU); 5 km. SW San Ignacio, 200 m., 8 (KU); 1 km. NE Santa Lucía, 3700 ft., 12 (KU); Santa Lucía, 3600 ft., 1 (KU); 1 mi. E Santa Lucía, 4200 ft., 5 (4 KU, 1 MSU); 2 mi. SW Santa Lucía, 3750 ft., 1 (MSU); Sierra de Choix, 50 mi. NE Choix [actually about 15 mi. NE Choix, see Goldman, 1951:251], 7 (USNM); 44 km. ENE Sinaloa, 600 ft., 12 (KU); 8 km. N, 22 km. E Sinaloa, 400 ft., 2 (KU); Sinaloa, 2 (USNM); 1 mi. E Sinaloa, 180 ft., 5 (KU); 10 km. S, 38 km. E Sinaloa, 800 ft., 5 (KU); 6 mi. NNW Teacapán, 3 (KU); Teacapán, Isla Palmito del Verde, 3 (KU); 13 km. NNE Vaca, 1300 ft., 1 (KU); 34 mi. NE Villa Unión on Mexican Hwy. 40, 1 (UA); 8 km. N Villa Unión, 450 ft., 11 (KU); 2 mi. W Villa Unión, 1 (KU); 18 mi. SE Villa Unión, 300 ft., 4 (CAS).

SONORA: near Alamos [8 mi. NW Alamos according to Goldman, 1951:253], 2 (USNM); Alamos, 54 km. E Navajoa, 1000 ft. [approximately 4 miles by road northwest of Alamos according to field notes of collector], 12 (KU); 1 mi. NW Alamos, 1500 ft., 1 (MVZ); Alamos, 12 (USNM); 1 mi. E Alamos, 1 (LACM); 9 mi. SE Alamos, 1 (KU); Camoa, Río Mayo, 5 (1 MVZ, 4 USNM); Chinobampo, 5 (UCLA); Guirocoba, 13 (4 LACM, 3 MVZ, 6 UCLA); 2 mi. E Guirocoba, 2 (MVZ); La Estancia, 6 mi. N Nacori, 2150 ft., 5 (MVZ); Las Delicias [±¼ mi. E of plaza], Alamos, 1 (UA); Matape, 105 km. E Hermosillo, 2300 ft., 3 (KU);

23 mi. S, 5 mi. E Nogales, 3200 ft., 1 (KU); Río Alamos, 1 (TTU); Río Cuchahaqui, 4 (TTU); E bank Río Yaqui, 1 mi. S El Novillo, 1 (UNM); Tecoripa, 3 (UCLA); Tesia, 14 (UCLA).

Additional records.—JALISCO: 5 mi. W Guadalajara (Ingles, 1959: 394); 10 mi. S Guadalajara (Ingles, 1959:394); Río Ameca (J. A. Allen, 1906:250). NAYARIT: 14 mi. S Acaponeta (Ivens *et al.*, 1959:54); 11 km. E Ixtlán del Río (Loomis, 1971:703). SINALOA: 11 mi. NE Copala (Levine *et al.*, 1958:295); 6.4 km. SW Copala, 230 m. (Kohls and Clifford, 1966:813); 35 mi. N Culiacán (Ingles, 1959:394); 22 km. N Culiacán (Loomis, 1971:100); 12 mi. NE El Fuerte (Wrenn and Loomis, 1967:160); 34 mi. N Mazatlán (Ivens *et al.*, 1959:54); 15 mi. N Mazatlán (Eisenberg, 1963*a*: 89); 8 km. WSW Mazatlán (Goodwin, 1954:10). SONORA: 13 km. W Alamos (Loomis, 1971:699); Ures (Burt, 1938:43).

Marginal records.—SONORA: 23 mi. S, 5 mi. E Nogales; E bank Río Yaqui, 1 mi. S El Novillo; 2 mi. E Guirocoba. CHIHUAHUA: near Batopilas [approximately 20 mi. W Batopilas according to Goldman, 1951:119]. SINALOA: 44 km. ENE Sinaloa; 20 km. N, 5 km. E Badiraguato. DURANGO: Chacala. SINALOA: 6 km. E Cosalá; 1 mi. E Santa Lucía. DURANGO: 2 mi. E Pueblo Nuevo. NAYARIT: La Cuchara, approx. 40 mi. E Acaponeta; Platanares, 10 mi. E Ruiz; 20 mi. SE Tepic; ½ mi. W Jalisco-Nayarit border on Mexican Hwy. 15. JALISCO: 1 mi. N Tequila; 9 mi. NNE Guadalajara; El Zapote; 7 mi. W Ameca. NAYARIT: Amatlán de Cañas; 1 mi. SW San José del Conde; Compostela; 17 mi. E San Blas; 17 km. SE Tuxpan and hence northward along the coast. SINALOA: 24 km. S Gusave. SONORA: Chinobampo; Tecoripa; Ures.

Liomys pictus pictus (Thomas, 1893)

1893. *Heteromys pictus* Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:233, September.
1911. *Liomys pictus*, Goldman, N. Amer. Fauna, 34:33, 7 September.
1902. *Liomys pictus rostratus* Merriam, Proc. Biol. Soc. Washington, 15:46, 5 March; holotype from near Ometepec, Guerrero.
1902. *Liomys pictus isthmius* Merriam, Proc. Biol. Soc. Washington, 15:46, 5 March; holotype from Tehuantepec, Oaxaca.
1902. *Liomys veraecrucis* Merriam, Proc. Biol. Soc. Washington, 15:47, 5 March; holotype from San Andrés Tuxtla, Veracruz.
1902. *Liomys obscurus* Merriam, Proc. Biol. Soc. Washington, 15:48, 5 March; holotype from Carrizal, Veracruz.
1902. *Liomys phaeura* Merriam, Proc. Biol. Soc. Washington, 15:48, 5 March; holotype from Pinotepa, Oaxaca.
1902. *Liomys orbitalis* Merriam, Proc. Biol. Soc. Washington, 15:48, 5 March; holotype from Catemaco, Veracruz.
1903. *Heteromys paralius* Elliot, Field Columb. Mus., Zool. Ser., 3:233, 3 September; holotype from San Carlos, Veracruz.
1956. *Liomys pinetorum* Goodwin, Amer. Mus. Novit., 1791:2, 28 September; holotype from San Miguel, about 4000 ft., 24 km. NE Tonalá, Cerro Tres Picos, District of Tonalá, Chiapas.

Holotype.—Adult female, skin and skull, BMNH 93.8.12.2, from San Sebastián, 4300 ft., Jalisco; obtained on 9 May 1893 by A. C. Buller. Skin in good condition but no external measurements listed; skull in good condition excepting terminal half of nasals and pterygoid wings missing.

Measurements of holotype.—Zygomatic breadth, 15.1; interorbital constriction, 7.6; mastoid breadth, 13.7; length of maxillary toothrow, 5.2; depth of braincase, 8.5; interparietal width, 8.8; interparietal length, 4.7.

Distribution.—Western México from Santiago, Nayarit, southward through coastal areas and Pacific slope of adjacent highlands of Jalisco, Colima, Michoacán, Guerrero, Oaxaca, and to Chiapas; occurring also in the region of the

Isthmus of Tehuantepec, in the central valley of Chiapas as far as Nentón, Guatemala, and in the lowlands of Veracruz north as far as San Carlos (Fig. 28).

Comparisons.—Liomys pictus pictus can be distinguished from *Liomys pictus plantinarensis* by its larger size, both externally and cranially (compare values of samples 7, 10, 12, 13, 18 with 11, 16, 17 in Table 11). The color of these two subspecies is essentially the same. A much higher percentage of individuals of *pictus* have the posterior margin of the interparietal unnotched than in *plantinarensis*. In Jalisco and Colima, some individuals of *plantinarensis* have the interparietal bone divided, but no individuals of *pictus* with this condition (Table 13) have been examined from that region.

Comparisons of *pictus* with *Liomys pictus annectens* and *Liomys pictus hispidus* are given in the accounts of those subspecies.

Remarks.—From the rather lengthy synonymy given above, it is evident that I have included in this subspecies several taxa that were formerly considered to be distinct. The primary work previously done on this group was by Goldman (1911:33-45), but his analysis was limited because he had only a small amount of material available for study. However, now with larger series and extensive material from areas that are intermediate between those from which Goldman had material, it becomes evident from the univariate and multivariate analyses that mice occurring in the lowlands of western México, Oaxaca, Chiapas, and Veracruz (samples 7, 10, 12, 13, 18, 19, 21, 24-29; see discussion of sample 14 below) represent a chain of morphologically similar populations that are best considered as a single taxon. This group of populations is characterized by medium size, undivided interparietal bone, relatively high number of individuals with posterior border of interparietal unnotched in northwestern populations grading to medium to low number in southern and eastern populations, and premaxillary bones terminating posterior to the nasal bones.

Goodwin (1956*b*:2-3) described *Liomys pinetorum* from Cerro Tres Picos, 24 km. NE Tonalá, Chiapas, on the basis of a single adult female. Goodwin distinguished *pinetorum* at the specific level from *pictus* on the basis of its large size; high, broad braincase that was nearly straight in side view; short rostrum; truncate nasals [actually the nasals are emarginate], not extending beyond posterior border of premaxillae; large, oval interparietal; small bullae; large, uncrowded molariform teeth. The measurements of the holotype of *pinetorum* are as follows: total length, 241; length of tail, 142; length of hind foot, 28.5; greatest length of skull, 33.3; zygomatic breadth, 15.5; interorbital constriction, 7.8; mastoid breadth, 14.8; length of nasals, 13.5; length of rostrum, 14.4; length of maxillary toothrow, 5.5; depth of braincase, 8.7; interparietal width, 9.1; and interparietal length, 5.0. Comparing these external and cranial measurements with those given in Table 11, it can be seen that all fall within the range of variation for *Liomys pictus* from the central valley of Chiapas (sample 26). Comparing the qualitative cranial characters with Tables 13 and 14 and with adult female specimens from Finca San Salvador, Chiapas (KU 102639-40), La Trinitaria, Chiapas (KU 61647-48), Madre Mía, Chiapas (AMNH 167409), Ocozocoautla, Chiapas (AMNH 171603), and La Mata, Oaxaca (AMNH 165997), it was found that those characters described as distinctive of *pinetorum* fall within the range of variation of the species *Liomys pictus*, and all characters could be matched in at least some of the specimens cited. Based on this information, I have concluded that *pinetorum* is a junior synonym of *pictus*.

The relationships of the *Liomys pictus* from Colima (sample 14) and southern Jalisco have proven to be an intriguing problem and one on which I can record only preliminary remarks because specimens are unavailable from certain critical areas and the material I have examined is not extensive. All specimens from coastal Colima and those from west of the Río Armería agree well with typical *L. p. pictus*. Also specimens from around the base of Volcán de Colima at Hacienda San Antonio and Quesaría in Colima and 2 km. NE San Marcos, Jalisco, are referable to *pictus*, but specimens from 6 km. S Atenqueque, only 5 kilometers north-northwest of the San Marcos locality, agree in all characteristics with *L. p. plantinarensis* and the type locality of *plantinarensis* is only 5 kilometers northeast of the locality at San Marcos. From extreme eastern Colima at Trapichillos, two subadult specimens are available for study. A subadult male has nearly reached adult size, judging from the form of the skull and fusion of the basioccipital-basisphenoid suture, and is definitely older than the female. Both of these specimens have small external and cranial measurements (male and female, respectively, total length 199, 170; greatest length of skull, 28.7, 27.8; mastoid breadth, 13.7, 13.2) and have other cranial characteristics suggestive of *L. p. plantinarensis* (such as the division of the interparietal bone in the male and notching of the posterior margin of interparietal bone in both specimens). I have placed these specimens in *plantinarensis* pending additional information on material from this area. It should also be pointed out in regard to this case that a large series of specimens from 15 km. SE Trapichillos at a place 14½ mi. S Pihuamo, Jalisco, agree closely with typical specimens of *plantinarensis*. When specimens from the vicinity of Colima City and southwestward along the eastern edge of the valley of the Río Armería are considered, subspecific allocation of specimens becomes extremely difficult because of the high degree of variation exhibited (see SE values for sample 14 in Table 11). Some specimens from this area are large and would appear to be assignable to *pictus*, others are small and would appear to be best arranged with *plantinarensis*, whereas a few appear to be intermediate in size and may represent intergradation between the two taxa. Of two adults from Colima (actually about 3 miles west of the city according to Goldman, 1951:135), one (USNM 33359/45387) is small (greatest length of skull 27.8), whereas the other (USNM 33362/45390) is of medium size (greatest length of skull 30.8) and approaches nearest to being intermediate in size between *pictus* and *plantinarensis* of any specimen that I have examined from this area. Again, one specimen from Las Lomas (approximately 3 or 4 mi. S Colima), one from 3 mi. SE Colima, and two from 23 km. SW Colima are small and approach *plantinarensis* in size (greatest length of skull, respectively, 29.5, 28.8, 29.3, 28.5, all specimens adults), but three specimens from 4 mi. SE Colima and a subadult from 4 mi. SW Colima are medium to large in size and would probably be best placed in *pictus* (greatest length of skull, respectively, 31.1, 32.6, 31.1, 30.0). The qualitative cranial characters cannot be considered as conclusive, but are more suggestive of *pictus* than *plantinarensis*. None of the specimens has divided interparietal bones, a condition found in about 20 per cent of the specimens of *plantinarensis*, but not in *pictus*, and at least in three of those specimens the nasals terminate at the same point as the premaxillaries, which is a characteristic found in no *plantinarensis* (sample 11), but in at least 10 per cent of the specimens of *pictus*. I have, for the present, considered this to be an area of intergradation between *pictus* and *plantinarensis* and assigned the specimens to *pictus*. Extremely useful information about the relationships of these mice could be obtained by an analysis of the characteristics of specimens from a transect that would roughly follow Mexican Highway 110 from southern Jalisco to Colima City, then down into the valley of Río Armería, and into the mountains to the west.

At three localities near Agua del Obispo, Guerrero (5½ km. N, 5¼ km. N, 5 km. N), *Liomys pictus pictus* and *Liomys irroratus* have been obtained at the same locality. However, P. L. Clifton stated in his field notes that specimens of *pictus* from 5¼ km. N Agua del Obispo were collected in moist wooded areas along a stream, whereas the *irroratus* were obtained in more open and drier areas. This same ecological separation also is seen between *irroratus* and *L. p. hispidus* in Jalisco. Specimens from the vicinity of Agua del Obispo (sample 19) occupy a geographic position intermediate between *L. p. pictus* of the coast (samples 13, 18, 21) and *L. p. annectens* occurring at higher elevations in Guerrero and Oaxaca (samples 20, 22, 23, 30) and the specimens show, especially in females, some morphological intermediacy between the two subspecies. In the multivariate analysis the females occupied an almost perfectly intermediate position, but the males fell much closer to the lowland *pictus*.

The species *Liomys pictus* and *Liomys salvini* have been collected from the same locality at three places in southeastern Oaxaca and northwestern Chiapas (Reforma, Oaxaca; 6 mi. NW Tonalá, Chiapas; Tonalá, Chiapas). Unfortunately, no notes are available describing the situations under which each species was collected. Males of *Liomys pictus* from this area (sample 25) are much larger than was expected and may represent a form of character displacement away from the somewhat smaller males of *Liomys salvini*. Females of *pictus* from this area fit well with those from surrounding populations (see section on specific relationships following species accounts).

Three other specimens of *Liomys pictus* need to be mentioned. Two of these are from 2 mi. S Puerto Vallarta, Jalisco, and were reported by Ingles (1959: 394-95) as *Liomys bulleri*. Although I have not seen these specimens, almost certainly they are examples of *Liomys pictus*, which is the only species occurring in coastal lowlands in this area (see account of *Liomys irroratus bulleri* for additional information on the distribution of that taxon). The other specimen is from 2 km. SE Zihuatanejo, Guerrero (KU 35325), and was reported by Hall and Kelson (1959:536) as *Liomys pictus parviceps*, which is considered herein as a synonym of *Liomys pictus plantinarensis*. However, this is a large specimen (greatest length of skull, 33.3) and possesses other characteristics typical of *pictus*.

For a discussion of the relationships between the subspecies *pictus* and *hispidus* in southern Nayarit, *pictus* and *plantinarensis* in the vicinity of the mouth of the Río Balsas, and *pictus* and *annectens* in southern Oaxaca, see the accounts of those subspecies.

Mean length of ear of 10 adult males and females of *pictus* from southwestern Jalisco was, respectively, 15.6 (14.0-17.0) and 16.0 (14.0-17.0). The mean weight of these same individuals was, respectively, 53.0 (45.0-69.5) and 45.9 (41.5-54.3).

Specimens examined (1408).—GUATEMALA: Nentón, Huehuetenango, 4 (USNM).

CHIAPAS: 5 mi. N Berriozábal, 1 (UMMZ); 17 mi. W Bochil, 1 (AMNH); ½ mi. N Cacahuatál, 1 (LACM); Cerro del Cañon del Sumidero, 2 mi. NNW Tuxtla Gutiérrez, 2000 ft., 2 (MVZ); near Cerro Hueco Cave, 2 mi. E Tuxtla Gutiérrez, 2600 ft., 1 (TCWC); Cerro Tres Picos, 1 (AMNH); 5 mi. S Chiapa, 1 (AMNH); Cinco Cerros, 8 (AMNH); Cintalapa, 30 (UMMZ); 35 mi. SE Comitán, 2 (AMNH); El Chorreadero, 6 km. NE Chiapa de Corzo, 740 m., 2 (UNAM); Finca San Salvador, 15 km. SE San Clemente, 1000 m., 11 (KU); 15 mi. S, 2 mi. E La Trinitaria, 5 (KU); Madre Mía, 1 (AMNH); Ocozocoautla, 9 (1 AMNH, 8 UMMZ); 12 mi. E Ortiz Rubio on Villa Flores Road, 1 (UA); Pan American Hwy., 16 mi. N Guatemalan border, 2 (AMNH); Puerta Arista, 1 (AMNH); Rancho Fernando, 42 km. W Cintalapa, 1 (UA); Rancho Santa Ines, 35 km. S Comitán, 790 m., 2 (UNAM); Río San Gregario at San Gregario, 30 mi. NW Ciudad Cuauhtémoc, 2000 ft., 3 (MVZ); San Bartolomé, 6 (USNM); Santo Domingo [near Cupia which is 4 km. SSE Chiapa de Corzo], *ca.* 1300 ft., 1 (TCWC); San Vincente, 1 (USNM); 6 mi. NW Tonalá, 4 (KU); Tonalá, 11 (5 AMNH, 6 USNM); 9 mi. SE, 8 mi. NE Tonalá, 3 (LACM); 1 mi. N Tuxtla Gutiérrez, 1 (UMMZ); 2 km. NW Tuxtla Gutiérrez, 1 (UNAM); 10 mi. W Tuxtla Gutiérrez, 800 ft., 1 (UMMZ); Tuxtla Gutiérrez, 14 (USNM); 4 mi. E Tuxtla Gutiérrez, 1600 ft., 1 (MVZ); 1 mi. S Tuxtla Gutiérrez, 3 (UMMZ); 6 mi. W, 2 mi. S Tuxtla Gutiérrez, 2 (KU); 6 mi. W, 3 mi. S Tuxtla Gutiérrez, 1 (KU); Valley of Jiquipilas, 3 (USNM); Villa Flores, 9 (UMMZ).

COLIMA: Agua Zarca, 6 km. N Puebla Juárez, 1 (LACM); Armería, 12 (USNM); 3 km. S Armería, 1 (LSU); Cerro China, 2 (LACM); *ca.* 2 mi. SE Cihuatlán (Jalisco), 1 (UA); 9 mi. NNE Colima, 1 (UA); 4 mi. NNE Colima, 4 (LACM); Colima, 13 (3 UMMZ, 10 USNM); 3 mi. SE Colima, 1400 ft., 1 (UMMZ); 4 mi. SW Colima, 1400 ft., 1 (KU); 4 mi. SE Colima, 8 (7 LACM, 1 UA); 23 km. SW Colima, 3 (CAS); 1 km. N Comatlán, 7 (UA); Hda. Magdalena, 7 (USNM); Hda. San Antonio, 2 (USNM); La Gloria, 29 km. W Pueblo Juárez, 5 (4 UA, 1 UNAM); Las Juntas, 26 km. W Pueblo Juárez, 1 (UNAM); Las Juntas, approx. 5 km. SE Pueblo Juárez, 2 (UA); Las Lomas, 2 (UA); 5 mi. N Manzanillo, 2 (KU); Paso del Río, 200 ft., 20 (UMMZ); Pueblo Juárez, 23 (20 LACM, 3 UNAM); Quesería, 1 (ENCB); Rancho San Miguel, *ca.* 4 km. SW Armería, 2 (UA); 6 mi. N Santiago, 1 (KU); 3 mi. N Santiago, 3 (KU); 4 mi. W, 1 mi. S Santiago, 10 ft., 1 (KU); 3 km. S Santiago, 1 (KU); 2 km. N Tlapeixtes, 1 (UA).

GUERRERO: ½ mi. W Acahuizotla, 26 (UMMZ); Acahuizotla, 24 (4 KU, 16 TCWC, 4 USNM); 2 mi. NW Acapulco, 50 ft., 1 (KU); Acapulco, 14 (USNM); 3 mi. S Acapulco, 1 (MWU); S side Acapulco Bay, 200 ft., 17 (UMMZ); 5½ km. N Agua del Obispo, 3400 ft., 6 (KU); 5¼ km. N Agua del Obispo, 3350 ft., 5 (KU); 5 km. N Agua del Obispo, 3250 ft., 19 (KU); 2½ km. N Agua del Obispo, 3100 ft., 4 (KU); 1 km. N Agua del Obispo, 3000 ft., 1 (KU); Agua del Obispo, 12 (9 KU, 1 TCWC, 1 UMMZ, 1 UNAM); 14 mi. S Chilpancingo, 3500 ft., 3 (CAS); 4 km. NE Colotilpa, 1100 m., 7 (ENCB); 1 mi. SW Colotilpa, 2700 ft., 4 (TCWC); 2 mi. SW Colotilpa, 2700 ft., 1 (TCWC); near Ometepec [approximately 9 mi. SE Ometepec according to Goldman, 1951:156], 8 (USNM); Pie de la Cuesta, 1 (UNAM); ½ mi. N Rincón, 2600 ft., 1 (TCWC); ½ mi. S Rincón, 1 (UNAM); 1 mi. S Rincón, 2600 ft., 4 (TCWC); Río Aguacatillo, 30 km. N Acapulco, 1000 ft., 6 (TCWC); Sihuatanejo Bay, 7 (UMMZ); 8 mi. SW Tierra Colorada, 600 ft., 1 (TCWC); 5 mi. (by road) E Zacatula, 50 m., 2 (UMMZ); 2 km. SE Zihuatanejo, 1 (KU).

JALISCO: 4 mi. NE Autlán, 3000 ft., 13 (UMMZ); 2½ mi. NNE Autlán, 2 (KU); Autlán, 1 (UNAM); 2 mi. SSE Autlán, 30 (KU); 6 mi. SW Autlán, 1 (MSU); 15 km. SW Autlán, 1 (CAS); 11 mi. SW Autlán, 2000 ft., 6 (KU); 5 mi. NE Barro de Navidad, 200 ft., 1 (KU); 3 mi. NW Barro de Navidad, 30 ft., 10 (KU); 5 km. NNW Barro de Navidad, 200 ft., 2 (KU); Chamela Bay, 5 (UMMZ); 15 km. NW Cihuatlán, 6 (KU); Cihuatlán, 15 ft., 1 (KU); Cuitzamala, 25 ft., 14 (KU); 14 km. S Durazno, 10 (KU); 2 km. NW Emiliano Zapata, 20 m., 3 (KU); Ixtapa, 6 (USNM); La Cuesta, 1900 ft., 4 (KU); 2 mi. S La Cuesta, 1500 ft., 3 (KU); La Cumbre, 4 (UA); 2 mi. SW La Resolana, 1100 ft., 14 (KU); 6 mi. E Limón, 2700 ft., 2 (KU); 7 mi. NE Melaque, 1 (LACM); 14 mi. NW Mascota, 6500 ft., 1 (KU); 12 mi. NW Mascota, 5800 ft., 1 (KU); 3 mi. N Mascota, 6100 ft., 1 (KU); 2 mi. N Milpillas, 3000 ft., 9 (KU); ½ mi. N Navidad, 5 (UMMZ); 3 mi. E Navidad, 50 ft., 3 (UMMZ); Navidad Bay, 1 (UMMZ); 4 mi. NNE Puerto Vallarta, 50 ft., 3 (KU); 4 mi. SW Puerto Vallerta, 20 ft., 6 (KU); 20 km. WNW Purificación, 1400 ft., 10 (KU); 2 mi. N Resolana, 1500 ft., 34 (UMMZ); Sal se Puedes, 1 (AMNH); 1 mi. N San Gabriel, 4000 ft., 2 (UMMZ); 2 km. NE San Marcos, 1 (UA); San Sebastián, 4400 ft., 35 (1 BMNH, 8 KU, 26 USNM); about 30 km. N, 10 km. E Santiago (Colima), 1 (KU); 7 mi. SE Tapalpa, 6300 ft., 2 (KU); 5 mi. SW Tecomate, 1000 ft., 6 (KU); 7½ mi. SE Tecomate, 1500 ft., 8 (KU); 2 mi. N Tenacatita, 25 ft., 2 (KU); Tenacatita Bay, 3 (UMMZ); Wakanakili Mts., 6 (AMNH).

MICHOACAN: 16 mi. S Arteaga, 800 ft., 4 (KU); 1 mi. E La Mira, 300 ft., 1 (KU); 8 km. N Melchor Ocampo, 80 m., 1 (ENCB).

NAYARIT: Aticama, 10 ft., 4 (KU); 5 mi. S Las Varas, 150 ft., 12 (KU); 8 mi. SSW Las Varas, 3 (KU); Navarrete, 1 (USNM); 11 mi. NE San Blas, 500 ft., 11 (MSU); 7 mi. ENE San Blas, 100 ft., 2 (KU); 5 mi. NE San Blas, 1 (UNAM); 4 mi. NE San Blas, 100 ft., 12 (UMMZ); San Blas, 1 (MSU); 1½ mi. E San Blas [Playa Matanchen], 1 (UA); 2 mi. E San Blas, 50 ft., 3 (1 MSU, 2 UMMZ); 3½ mi. E San Blas, 100 ft., 17 (UMMZ); 4 mi. E San Blas, 100 ft., 27 (MSU); 5 mi. E San Blas, 1 (UNAM); 8 mi. E San Blas, 5 (LACM); 10 mi. E San Blas, 8 (LACM); 5 mi. SE San Blas, 7 (KU); 4 mi. S, 5 mi. E San Blas, 3 (UNM); 1 mi. S San Francisco, 50 ft., 2 (KU); Santiago, 5 (USNM); 2 mi. WNW Valle de Banderas, 6 (KU).

OAXACA: Agua Blanca, 6 (AMNH); Aguaje Guayabo, 2 (AMNH); Aguaje las Animas, 2 (AMNH); Aguaje Sapotal, 1 (AMNH); Aguaje Tres Cabezas, 4 (AMNH); Angeles Bay, 4 (UMMZ); Buena Vista 3 (AMNH); Cerro Calderona, 1 (AMNH); Cerro de Potosi, Chahuites, 1 (AMNH); Cerro Guacomaya, San Juan Acaltepec, 1 (AMNH); Cerro Ocotepec, 1 (AMNH); Cerro Palaa de Oro, 2 (AMNH); Cerro San Pedro, 7 (AMNH); Cerro Tigre, 5 (AMNH); Cerro Verde, 1 (AMNH); Chacalapa, 12 (KU); Chicapa, 1 (USNM); Cycad Camp, km. 233 on Oaxaca-Puerto Escondido Road, 2 (CAS); El Bambita, 1 (AMNH); El Campanario, 2 (AMNH); Escondido Bay, 2 (UMMZ); Escurano, 15 (AMNH); Guichicovi, 7 (USNM); Guichina, 5 (AMNH); Guiengola, 5 (AMNH); Huilotepec, 3 (USNM); Ixcuintepec, 2 (AMNH); Jalapa, 2 (AMNH); Jamiltepec, 3 (AMNH); 7 mi. E Juchitán, 1 (KU); Lagunas, 5 (4 FMNH, 1 USNM); Laguna Sol y Luna, 1 (AMNH); La Mata, 1 (AMNH); Las Minas, 5 mi. E Tapanatepec, 5 (UA); Las Tejas, 1 (AMNH); 20 mi. NW La Ventosa, 3 (AMNH); Limón, 1 (AMNH); Llano Grande, 7 (USNM); Mixtequilla, 2 (AMNH); Nejapa, 85 km. WNW Tehuantepec, 500 m., 8 (UMMZ); 37 km. SE Nejapa, 2850 ft., 1 (CAS); Nizanda, 2 (ANMH); Ocotita, 2 (AMNH); Pinotepa, 2 (USNM); Pinotepa de Don Luis, 5 (AMNH); Portillo Guayabo, 4 (AMNH); Portillo Zapote, 1 (AMNH); Pozo Río, 3 (AMNH); 1 mi. W Puerto Angel, 9 (UMMZ); Puerto Angel, 22 (13 KU, 9 USNM); Reforma, 18 (8 FMNH, 10 UMMZ); Río Chile, Tequisistlán, 1 (AMNH); Salazar, 9 (AMNH); 8 km. NW Salina Cruz, 2 (ENCB); 4 km. NNE Salina Cruz, 1 (UNAM); Salina Cruz, 1 (AMNH); San Antonio, 2 (AMNH); San Bartolo, 3 (USNM); San Bartolo Yautepec, 2 (AMNH); San José Lachiguirí, 1 (AMNH); San Juan la Jarcia, 1 (AMNH); San Miguel Caja de Agua, 1 (AMNH); San Pedro Jilotepec, 1 (AMNH); Santa Cruz Bay, 13 (UMMZ); Santa Efigenia, 14 (USNM); Santa Lucía, 16 (AMNH); Santa María Ecatepec, 8 (AMNH); Santiago Lachiguiń, 3 (AMNH); Santo Domingo, 5 (USNM); Sierra Madre, [15 mi.] N Zanatepec, 2 (AMNH); 20 mi. W Tapanatepec on Mexican Hwy. 190, 1 (UA); 2½ mi. W Tapanatepec, 2 (UMMZ); Tapanatepec, 1 (AMNH); 60 mi. NW Tehuantepec, 3 (AMNH); 30 mi. N Tehuantepec, 1 (AMNH); 12 km. NW Tehuantepec, 200 m., 4 (ENCB); near Tehuantepec [approximately 8 mi. NW Tehuantepec along the Río Tehuantepec at the base of Cerro de Giengola according to Goldman, 1951:226], 14 (USNM); 9 km. NW Tehuantepec, 100 m., 2 (ENCB); 10 mi. W, 2 mi. N Tehuantepec, 200 ft., 3 (KU); 2 mi. WNW Tehuantepec, 200 ft., 5 (UMMZ); 16 km. W Tehuantepec, 5 (UNAM); 10 mi. W Tehuantepec, 300 ft., 5 (UMMZ); Tehuantepec, 65 m., 18 (2 UMMZ, 16 USNM); Vincente, 5 (UMMZ); Zanatepec, 2 (AMNH).

VERACRUZ: Achotal, 1 (FMNH); 8 mi. N Alvarado, 1 (AMNH); 7 mi. N Alvarado, 8 (AMMH); 6 mi. N Alvarado, 3 (AMNH); 5 mi. N Alvarado, 4 (2 AMNH, 2 UNAM); 8 mi. W Alvarado, 1 (AMNH); 7 mi. W Alvarado, 4 (AMNH); 6 mi. W Alvarado, 1 (AMNH); Alvarado, 10 (AMNH); Boca del Río, 10 ft., 9 (4 KU, 5 TCWC); Carrizal, 2 (USNM); Catemaco, 9 (USNM); 1 km. E Catemaco, 1 (ENCB); 1½ km. E Catemaco, 6 (ENCB); 5 mi. S Catemaco, 2 (KU); 20 km. SE Cerro Gordo, 3 (UNAM); 14 km. SW Coatzacoalcos, 100 ft., 2 (KU); Jimba, 350 ft., 1 (KU); Lago Catemaco, 1 (UNAM); Otatitlán, 8 (USNM); 2 km. N Paraje Nuevo, 1700 ft., 1 (KU); Pasa Nueva, 11 (AMNH); 4 km. W Paso de San Juan, 250 ft., 1 (KU); 3 mi. NW Plan del Río, 1000 ft., 1 (UMMZ); ½ mi. NW Plan del Río, 900 ft., 1 (UMMZ); ½ mi. E Plan del Río, 600 ft., 1 (UMMZ); 3 km. N Presidio, 1500 ft., 2 (KU); Puente Nacional, 6 (5 KU, 1 TCWC); Río Blanco, 20 km. WNW Piedras Negras, 10 (KU); Río Blanco, 20 km. W Piedras Negras, 2 (KU); San Andrés Tuxtla, 4 (USNM); 3 km. E San Andrés Tuxtla, 1000 ft., 32 (KU); San Carlos, 11 (10 FMNH, 1 USNM); 15 km. ESE San Juan de la Punta, 400 ft., 2 (KU); Santa María, 4 (USNM); 40 mi. S Veracruz, 1 (AMNH).

Additional records.—CHIAPAS: 3 mi. E Arriaga (Booth, 1957:11); 23 mi. S Comitán (Booth, 1957:12); 30 mi. S Comitán (Booth, 1957:11); Jaltenango (Wagner, 1961:207); Pan American Highway at Río San Gregario (Furman, 1955:525; Brennan and Jones, 1959:427). COLIMA: 10 mi. S Manzanillo (Ingles, 1959:394). GUERRERO: Zacatula (Alvarez, 1968:31). JALISCO: 2 mi. S Puerto Vallarta (Ingles, 1959:395—reported as *Liomys bulleri*). NAYARIT: 7 km. E San Blas (Loomis, 1971:703); 9 km. E San Blas (Loomis, 1971:703); 14 km. E San Blas (Loomis, 1971:703). OAXACA (Goodwin, 1969:143-144 unless otherwise noted): Cerro Sombrerito; Chontecomatlán; Gueladú; Isthmus of Tehuantepec, 8 mi. S Veracruz-Oaxaca state line; La Chacahua; Las Cuevas; Río Grande; 2 mi. W Tapantepec (Hubbard, 1958:165); Tenango; 6 km. NE Tequisistlán (Monés, 1971:170); Zarzamora. VERACRUZ: Orizaba (Hall and Dalquest, 1963:284); Plan del Río (Davis, 1944:390); Santiago Tuxtla (Goldman, 1911:43).

Marginal records.—NAYARIT: Santiago; *Navarrete*; *10 mi. E San Blas*; 5 mi. S Las Varas. JALISCO: San Sebastián; 3 mi. N Mascota; La Cuesta; 7 mi. SE Tapalpa; 1 mi. N San Gabriel; *2 km. NE San Marcos*. COLIMA: Queseña; 4 mi. SE Colima; 23 km. SW Colima. MICHOACAN: 16 mi. S Arteaga; 8 km. N Melchor Ocampo. GUERRERO: *Zacatula;* 5 mi. (by road) E Zacatula; 2 km. SE Zihuatanejo; 5½ mi. N Agua del Obispo; 4 km. NE Colotilpa; near Ometepec [approximately 9 mi. SE Ometepec according to Goldman, 1951:156]. OAXACA: Llano Grande; Pinotepa de Don Luis; Jamiltepec; Cycad Camp, km. 233 on Oaxaca-Puerto Escondido Road; Chacalapa; San Bartolo Yautepec; Nejapa, 60 mi. NW Tehuantepec; Ixcuintepec; San José Lachiguirí; Guichicovi; 8 mi. S Veracruz-Oaxaca state line. VERACRUZ: Achotal; Jimba; Otatitlán. OAXACA: Vincente. VERACRUZ: 2 km. N Paraje Nuevo; 3 mi. NW Plan del Río; San Carlos; hence south along the coast to a point 14 km. SW Coatzacoalcos. CHIAPAS: 17 mi. W Bochil; El Chorreadero, 6 km. NE Chiapa de Corzo; San Bartolomé; San Vincente. GUATEMALA: Nentón. CHIAPAS: 35 mi. SE Comitán; Jaltenango; Villa Flores; 9 mi. SE, 8 mi. NE Tonalá; *Madre Mía*; Puerto Arista; hence northward along the west coast of México. NAYARIT: San Blas.

Liomys pictus plantinarensis Merriam, 1902

1902. *Liomys plantinarensis* Merriam, Proc. Biol. Soc. Washington, 15:46, 5 March.
1911. *Liomys pictus plantinarensis,* Goldman, N. Amer. Fauna, 34:37, 7 September.
1904. *Liomys parviceps* Goldman, Proc. Biol. Soc. Washington, 17:82, 21 March; holotype from La Salada, 40 mi. S Uruapan, Michoacán.

Holotype.—Adult female, skin and skull, USNM 45630/33595, from Platanar [spelled Plantinar on specimen label], Jalisco, obtained on 4 April 1892 by E. W. Nelson and E. A. Goldman. Skin and skull in good condition.

Measurements of holotype.—Total length, 202; length of tail, 102; length of hind foot, 26; greatest length of skull, 29.4; interorbital constriction, 7.4; mastoid breadth, 13.0; length of nasals, 11.8; length of maxillary toothrow, 5.0; interparietal width, 8.4; interparietal length, 3.7.

Distribution.—This subspecies is confined mainly to the basins of interior drainage of southeastern Jalisco and western Michoacán and in the drainages of the Río Coahuayana in southern Jalisco and eastern Colima, Río Tepalcatepec in Michoacán, Río Balsas in Guerrero and their tributaries (Fig. 28). Some specimens, such as those from the vicinity of Coalcomán and Tumbiscatio, Michoacán, and El Limón, Guerrero, are from near the headwaters of rivers that flow directly into the Pacific Ocean.

Comparisons.—*Liomys pictus plantinarensis* can be distinguished from *Liomys pictus annectens* by its extremely small size both externally and cranially (compare values for samples 11, 16, 17 with 22, 23 in Table 11) and much paler dorsal coloration and paler orange lateral stripe. Only slight differences were observed between these two subspecies in qualitative cranial characters; the most noticeable difference was in the shape of the posterior end of the nasals in which a truncate termination was found in only one individual of *plantinarensis* but 11.5 and 25.0 per cent of the individuals from samples 22 and 23, respectively (Table 14).

From *Liomys pictus hispidus,* the subspecies *plantinarensis* can be distinguished by its small external and cranial dimensions (compare values for samples 11, 16, 17 with 1-6 in Table 11). Although specimens of *plantinarensis* are the smallest of the species, some specimens of *hispidus,* especially noticeable in males from sample 6, do approach their small size. Although some individuals of *plantinarensis* have an interparietal bone that is divided, these are mainly confined to sample 11, and even there the percentage of individuals with this condition is less than in populations of *hispidus* (Table 13). Only one specimen of *plantinarensis* examined possessed premaxillary and nasal bones that terminated at the same level, whereas this condition is common in *hispidus* (Table 14).

Comparison of *plantinarensis* with *Liomys pictus pictus* is given in the account of that subspecies.

Remarks.—Members of the subspecies *Liomys pictus plantinarensis* are the smallest of the species (see values for samples 11, 16, 17 in Table 11). In addition to small size, *plantinarensis* is distinguishable from contiguous populations of *pictus* on the basis of having only a few individuals with the posterior margin of the interparietal bone unnotched and a low percentage of individuals with the nasal bones truncate (Tables 13, 14). The external and cranial measurements of specimens from throughout the geographic range of the subspecies in both the univariate and multivariate analyses exhibit a small clinal decrease with decreasing latitude; the largest individuals are from southern Jalisco and northwestern Michoacán and the smallest occur along the Río Balsas in Guerrero. Although the name *parviceps* has previously been applied to these somewhat smaller southern populations, I believe that their relationships are best expressed by referring them to *plantinarensis*.

The number of plantar tubercles is a constant character within most species of the genus, but individuals of *plantinarensis* from southern Jalisco and probably adjacent areas of Michoacán exhibit a hlgh degree of variability in development of a sixth tubercle that is characteristic of other members of the species. In freshly killed specimens that I have examined, there may be no sixth tubercle as is the case in KU 120591 from 4 km. W Tuxpan and also the holotype (according to Goldman, 1911:38), or a darkly pigmented area lacking tubercular development as in KU 120590 from 4 km. NE Contla, or development of a small tubercle as in KU 97190 from 3½ mi. WNW Zapoltitic and KU 97213 from 2 7/10 mi. WNW Zapoltitic.

In the vicinity of the mouth of the Río Balsas, the geographic range of *L. p. plantinarensis*, which is evidently following the courses of the river and its tributaries in this area, nearly reaches the coastal plain and thereby would divide the range of *L. p. pictus*. Specimens from 4 km. N Infiernillo and El Atuto in Michoacán are typical representatives of *plantinarensis* and these are only approximately 27 kilometers from the Pacific. However, a specimen from 8 km. N Melchor Ocampo, which is from approximately 15 kilometers south of these specimens and nearer the coast, is large and has other cranial characters that clearly place it with *pictus* (although Alvarez, 1968:31, assigned it to *parviceps*) as is another specimen from La Mira, Michoacán. Although the geographic range of *pictus* is reduced to a relatively narrow band along the coast in the vicinity of the mouth of the Río Balsas it seems that at least limited gene flow is maintained by populations of *pictus* across this area.

In southern Jalisco, *L. p. plantinarensis* has been taken at two localities (3½ mi. WNW Zapoltitic and 2 7/10 mi. WNW Zapoltitic) with *Liomys irroratus jaliscensis* in a habitat that can be best described as the weedy edge of an old field. The two species have been obtained in Guerrero in three places (Iguala, 3200 m. SSE Iguala, and 2 km. ENE Los Sabinos) along the northern edge of the Balsas Valley and at one place (1½ mi. SE Zumpango) along the southern edge of the valley. However, as Hooper and Handley (1948:2) pointed out earlier, *Liomys pictus* appears to be the only species that occurs in the Balsas Valley below 2000 feet. At three localities northeast of Contla, Jalisco, specimens of *plantinarensis* have been taken in the same trapline with *Liomys spectabilis* and so far as I have been able to ascertain from trapping in the area, the two species occur in what appears to be the same type of habitat.

Ten adult males and 10 nonpregnant, adult females from southeastern Jalisco had, respectively, the following mean character values: length of ear, 14.0 (13.0-15.0) and 13.7 (13.0-14.5); weight, 43.9 (35.8-51.9) and 33.2 (24.3-45.7).

Specimens examined (321).—COLIMA: Trapichillos, 2 (UA).

GUERRERO: Apaxtla, 1350 m., 5 (UMMZ); Arroyo Alcholoya, 7 3/10 km. N Teloloapan, 1480 m., 3 (UNAM); El Limón, 9 (USNM); Iguala, 730 m., 40 (UMMZ); 3200 m. SSE Iguala, 970 m., 1 (UNAM); 2 km. ENE Los Sabinos, 1400 m., 3 (2 KU, 1 UNAM); Los Sabinos, 1210 m., 7 (KU); 2½ mi. W Mexcala, 2100 ft., 4 (TCWC); Río Balsas, 5 (USNM); 1½ mi. SE Zumpango, 4000 ft., 1 (TCWC).

JALISCO: 6 km. S Atenqueque, 4 (LACM); 3 3/10 mi. NE Contla, 3900 ft., 2 (KU); 3 mi. NE Contla, 3850 ft., 1 (KU); 2 2/10 mi. NE Contla, 3850 ft., 12 (KU); 4 km. NE Contla, 1340 m., 1 (KU); 1 8/10 mi. NE Contla, 3800 ft., 4 (KU); 1 3/10 mi. NE Contla, 3800 ft., 1 (KU); 9/10 mi. NE Contla, 3800 ft., 2 (KU); Jilotlán de los Delores, 2400 ft., 5 (KU); 8 mi. E Jilotlán de los Delores, 2000 ft., 24 (KU); Piguamo, 1 (UNAM); 14½ mi. S Pihuamo, 1100 ft., 10 (KU); Platanar, 1 (USNM); 4 km. NE Tamazula, 3800 ft., 16 (KU); 13 km. SW Tamazula, 3800 ft., 1 (KU); 8 km. N Tecalitlán, 4000 ft., 2 (KU); 4 km. W Tuxpan, 1380 m., 4 (KU); 3½ mi. WNW Zapoltitic, 5100 ft., 3 (KU); 2 7/10 mi. WNW Zapoltitic, 5000 ft., 18 (KU).

MICHOACAN: Agua Blanca, 1 (FMNH); 10 km. W Apatzingán, 1040 ft., 13 (FMNH); Apatzingán, 500 m., 5 (UMMZ); 10 mi. S, 1 mi. W Apatzingán, 800 ft., 10 (KU); ½ mi. W Coalcomán, 1 (UMMZ); Coalcomán, 2 (UNAM); ½ mi. SE Coalcomán, 3600 ft., 1 (UMMZ); 11 mi. by road E Dos Aguas, 4 (UMMZ); El Atuto, 3 km. NE Infiernillo (Guerrero), 1 (UNAM); 4 km. N Infiernillo (Guerrero), 1 (ENCB); near La Huacana, 3 (USNM); La Salada, 13 (USNM); Los Reyes, 13 (USNM); south bank Río de Tepalcatepec, 17 mi. S Apatzingán, 800 ft., 1 (KU); 1 mi. E, 2½ mi. S Tacámbaro, 4700 ft., 4 (MVZ); 4 mi. S, 1 mi. E Tacámbaro, 5 (MVZ); 1 mi. E, 6 mi. S Tacámbaro, 6 (MVZ); 7 mi. S Tumbiscato, 2700 ft., 10 (KU) 3 6/10 mi. by road S Tzitzio, 1 (UMMZ); 12 mi. S Tzitzio, 1050 m., 34 (UMMZ).

Marginal records.—JALISCO: 3 mi. NE Contla. MICHOACAN: Los Reyes; Apatzingán; near La Huacana; 1 mi. E, 2½ mi. S Tacámbaro; 3 6/10 mi. by road S Tzitzio; Agua Blanca. GUERRERO: Arroyo Alcholoya, 7 3/10 km. N Teloloapan; 2 km. ENE Los Sabinos; *Iguala*; 3200 m. SSE Iguala; 1½ mi. SE Zumpango; Río Balsas; El Limón. MICHOACAN: El Atuto, 3 km. NE Infiernillo; 7 mi. S Tumbiscato; 11 mi. by road E Dos Aguas; ½ mi. W Coalcomán. COLIMA: Trapichillos. JALISCO: Piguamo [=Pihuamo]; 6 km. S Atenqueque; 3½ mi. WNW Zapoltitic.

Liomys spectabilis

Jaliscan Spiny Pocket Mouse

This species is known from a restricted area in southeastern Jalisco. At present, the northernmost record of the species is from 8.5 mi. S Mazamitla and the southernmost is from 8 mi. SW Tecalitlán.

Diagnosis

External and cranial measurements large; no unworn permanent premolars are available, but premolar appears to resemble that of *L. pictus*; baculum long with a small rounded base; distal end of shaft with ventral keel that is laterally compressed; shaft dorsoventrally compressed posterior to terminal keel; glans penis short when compared with baculum; tip of glans long, glans only slightly sculptured; urethral lappets trilobed; 2N = 48; FN = 64; head of spermatozoon long and with pointed apex; distinct neck between head and midpiece of spermatozoon; wings of pterygoids narrow; six plantar tubercles; upper parts reddish brown; lateral stripe ochraceous; underparts white; hairs on back not curled upward so as to be conspicuous above spines.

Comparisons

Specimens of *Liomys spectabilis* can be distinguished from those of *Liomys salvini* by larger external and cranial measurements. Dental differences probably are similar to those between *pictus* and *salvini*. The baculum of *spectabilis* has a keel on the ventral side of the distal end of the shaft, whereas this feature is lacking in *salvini*; both species have a section of the shaft of the baculum that is dorsoventrally flattened. The glans penis of *spectabilis* can be distinguished from that of *salvini* by its shorter length in comparison with the length of the baculum, longer tip, and less external sculpturing. The urethral lappets of *spectabilis* are trilobed, whereas those of *salvini* are bilobed. *L. spectabilis* has 48 chromosomes with a fundamental number of 64, whereas *salvini* has 56 chromosomes with a fundamental number of 86. The spermatozoon of *spectabilis* has a long head with a pointed apex, whereas that of *salvini* is short with a blunt, broadly rounded apex. The upper parts of specimens of *spectabilis* are reddish brown with an ochraceous lateral stripe, but *salvini* has chocolate brown to somewhat paler brown upper parts with no lateral stripe; the hairs on the back of specimens of *salvini* are curled upward and are visible above the spines, but this is not true of specimens of *spectabilis*.

Liomys spectabilis can be distinguished from *Liomys adspersus* by its slightly smaller external and cranial measurements (except for interorbital constriction and interparietal width, which are wider in *spectabilis*). Dental differences probably are similar to differences between *pictus* and *adspersus*. The baculum of *spectabilis* has a keel on the ventral side of the distal end of the shaft, whereas in *adspersus* this is lacking; both species have a section of the shaft of the baculum that is dorsoventrally flattened. The glans penis of *spectabilis* can be distinguished from that of *adspersus* by its shorter length in comparison with the length of the baculum, longer tip, and less external sculpturing. The urethral lappets of *spectabilis* are trilobed, whereas those of *adspersus* are bilobed. The karyotype of *spectabilis* consists of 48 chromosomes with a fundamental number of 64, whereas *adspersus* has 56 chromosomes with a probable fundamental number of 84. The spermatozoon of *spectabilis* has a long head with a pointed apex, whereas that of *adspersus* is short with a blunt, broadly rounded apex. The upper parts of specimens of *spectabilis* are reddish brown with an ochraceous lateral stripe, but *adspersus* has chocolate brown to somewhat paler brown upper parts with no lateral stripe; the hairs on the back of specimens of *adspersus* are curled upward and are visible above the spines, but this is not true of specimens of *spectabilis*.

For comparisons of *L. spectabilis* with *L. irroratus* and *L. pictus*, see the accounts of those species.

Ecology

Relatively little is known about the ecology of *L. spectabilis*, the species being known presently only from eight localities in a restricted area of southeastern Jalisco. The known altitudinal range is from 3150 feet north of Pihuamo to 5300 feet south of Mazamitla. Nothing is known about the conditions under which the specimens from near Pihuamo and Tecalitlán were taken; three of the remaining six localities are discussed below.

8 1/2 mi. S Mazamitla, 5300 ft., Jalisco.—On the evening of 3 March 1964, P. L. Clifton set traps along a brush fence between a cornfield and a grove of oak. In addition to three specimens of *Liomys spectabilis*, only three *Peromyscus boylii* were taken at this site.

6 km. NE Contla, 1310 m., Jalisco.—The area northeast of Contla is under heavy agricultural use. All trapping was done in the immediate vicinity of a highway, which follows a shallow valley northeastward from Contla. The road right-of-way is about 40 to 50 feet wide at most points and has been allowed to grow to weeds, low brush, and trees; cornfields were located beyond the right-of-way in relatively level areas. Around the edges of these cornfields were rock or wire fences that were heavily overgrown with weeds and brush. On adjacent hillsides, where the slope became too steep to plant corn, the grass was heavily grazed in most places and was interspersed with clumps of dense, low brush. On the evening of 7 August 1969 Larry C. Watkins, Elmer C. Birney and I set traps along the roadside and in one of the hillside pastures. Small mammals that we obtained included *Liomys spectabilis*, *Oryzomys palustris*, and *Baiomys taylori*.

2.2 mi. NE Contla, 3850 ft., Jalisco.—The habitat at this locality resembles that described above for 6 km. NE Contla. On the evening of 19 September 1963, and again on 25 and 26 September, P. L. Clifton trapped in this area. He placed his traps along the fences around the cornfields and on adjacent hillsides. In addition to *Liomys spectabilis*, specimens of *Liomys pictus plantinarensis* and *Baiomys taylori* were obtained.

Geographic Variation

Univariate and Multivariate Analyses

Because only 21 specimens of this species are known, it was impossible to undertake univariate and multivariate analyses of geographic variation as done with the other species. External and cranial measurements of the known adults are given in Table 19.

Values for this species were included in the multivariate analyses of samples of *Liomys pictus* (see Figs. 21, 23-26). On the phenetic distance phenograms for

TABLE 19.—*Standard statistics for the known adult specimens of* Liomys spectabilis.

Catalog number or specimens averaged and sex	Mean	Range	2 SE
	Total length		
KU 96051, male (holotype)	280.0		
MSU 11496, male	270.0		
Four females	249.5	(242.0-261.0)	8.35
	Length of tail		
KU 96051, male	142.0		
MSU 11496, male	131.0		
Four females	129.0	(122.0-134.0)	5.03
	Length of hind foot		
Three males	30.7	(30.0-31.0)	0.67
Eight females	30.4	(29.5-32.0)	0.55
	Greatest length of skull		
Three males	35.0	(34.7-35.2)	0.30
Eight females	34.1	(33.0-35.3)	0.59
	Zygomatic breadth		
KU 96051, male	16.3		
KU 120606, male	15.2		
Six females	15.6	(14.8-16.0)	0.37
	Interorbital constriction		
Three males	8.2	(8.1-8.2)	0.07
Eight females	8.0	(7.5-8.4)	0.21
	Mastoid breadth		
Three males	14.6	(13.9-15.1)	0.72
Eight females	14.5	(14.0-15.4)	0.33
	Length of nasals		
Three males	14.5	(14.0-15.5)	0.97
Eight females	13.6	(12.6-14.2)	0.40
	Length of rostrum		
KU 96051, male	16.0		
KU 120606, male	15.8		
Eight females	15.5	(14.8-16.2)	0.35
	Length of maxillary toothrow		
KU 96051, male	5.0		
KU 120606, male	5.4		
Eight females	5.2	(5.0-5.6)	0.12

Table 19.—*Continued.*

	Depth of braincase		
KU 96051, male	8.6		
KU 120606, male	8.5		
Seven females	8.4	(8.2-8.6)	0.12
	Interparietal width		
Three males	9.0	(8.7-9.2)	0.29
Eight females	8.5	(7.8-9.0)	0.28
	Interparietal length		
Three males	4.8	(4.6-4.9)	0.18
Eight females	4.4	(4.0-4.8)	0.19

males and females, specimens of *Liomys spectabilis* (marked LS) are grouped with samples 22 and 23, which are *L. p. annectens. Liomys spectabilis* is far "distant" from sympatric populations (11) of *L. p. plantinarensis* and samples of *L. p. pictus* (10, 12, 13) from western Jalisco. On the two and three-dimensional projections for males the sample of *Liomys spectabilis* is located to the far right along component I, which is principally a function of size. For females, these projections show the sample of *L. spectabilis* nearer to samples 19, 20, 22, and 23 with sample 30, which is composed of four old adult females from Omilteme, Guerrero, at the far right of the plot. Again, it should be noted that *spectabilis* is far removed phenetically from the population of *pictus* (11) that occurs sympatrically with it and from other samples of *pictus* from Jalisco (10, 12, 13). Phenetically *L. spectabilis* most nearly resembles *L. p. annectens,* from which it is geographically far removed.

Qualitative Cranial Characters

All specimens examined (17) had the interparietal bone undivided. Of the 17 specimens examined, 77.8 per cent had the posterior margin of the interparietal bone unnotched, 16.7 per cent had a slight notch in the posterior margin of the interparietal bone, and 5.5 per cent had a large notch in the posterior margin of the interparietal bone. Of 17 specimens examined, 64.7 per cent exhibited nasal bones that terminated in an emarginate shape, 23.5 per cent were rounded terminally, and 11.8 per cent had nasals that were truncate posteriorly. Of 17 individuals that were examined, 88.2 per cent had premaxillary bones that terminated posterior to the end of the nasals and 11.8 per cent had nasal and premaxillary bones that terminated at the same level.

Variation in Color

From Table 20, it can be seen that specimens of *L. spectabilis* have significantly lower color reflectance values than do specimens of *Liomys pictus plantinarensis,* which occurs sympatrically with *spectabilis.* Specimens of *L. p. pictus* from the mountains of northwestern Jalisco have slightly higher readings than

TABLE 20.—*Color reflectance values of the middorsal region of four taxa of* Liomys.

Taxa	N	Red	Green	Blue
L. spectabilis	13	11.0	6.3	5.8
L. pictus plantinarensis	20	14.6	7.9	7.1
L. pictus pictus	8	12.3	6.4	5.5
L. pictus annectens	13	10.7	5.5	5.2

spectabilis for red and green and slightly lower for blue. The values for specimens of *L. p. annectens* are lower than those for *spectabilis* for all three colors, indicating these rats are slightly darker than *spectabilis*.

Taxonomic Conclusions

Liomys spectabilis is a monotypic species occupying a restricted geographic range in southeastern Jalisco. Its relationships are clearly with *Liomys pictus* (phenetically, it most closely resembles *L. p. annectens* based upon mensural data). However, *spectabilis* differs from *pictus* in details of karyology, bacular morphology, and sperm morphology.

Liomys spectabilis Genoways

1971. *Liomys spectabilis* Genoways, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 5:1, 18 June.

Holotype.—Adult male, skin and skull, KU 96051, from 2.2 mi. NE Contla, 3850 ft., Jalisco, obtained on 20 September 1963 by Percy L. Clifton. Skin and skull in good condition.

Measurements of holotype.—Total length, 280; length of tail, 142; length of hind foot, 31; length of ear, 17; greatest length of skull, 35.1; zygomatic breadth, 16.3; interorbital constriction, 8.2; mastoid breadth, 15.1; length of nasals, 14.0; length of rostrum, 16.0; length of maxillary toothrow, 5.0; depth of braincase, 8.6; interparietal width, 9.2; interparietal length, 4.6; weight, 69.3.

Distribution.—Restricted to southeastern Jalisco (Fig. 30).

Comparisons.—see above.

Remarks.—Although *Liomys spectabilis* is obviously most closely related to *Liomys pictus*, the two species are presently known to occur sympatrically at three localities as follows: 3.3 mi. NE Contla (four specimens of *spectabilis* and two specimens of *plantinarensis*), 3 mi. NE Contla (one *spectabilis* and one *plantinarensis*), and 2.2 mi. NE Contla (seven *spectabilis* and 11 *plantinarensis*). *L. spectabilis* occupies a restricted distribution near the eastern limit of the geographic range of *L. pictus* in Jalisco. It seems plausible that the precursor of these two species occurred throughout this area of México, and that the parental stock was split into two parts in response to changing environmental conditions. One segment probably was restricted to coastal regions of western México and gave rise to *L. pictus*, whereas the other was isolated in interior Jalisco and gave rise to *L. spectabilis*. Subsequent to speciation, *L. pictus* has reinvaded inland areas of Jalisco and now occurs sympatrically with *spectabilis*.

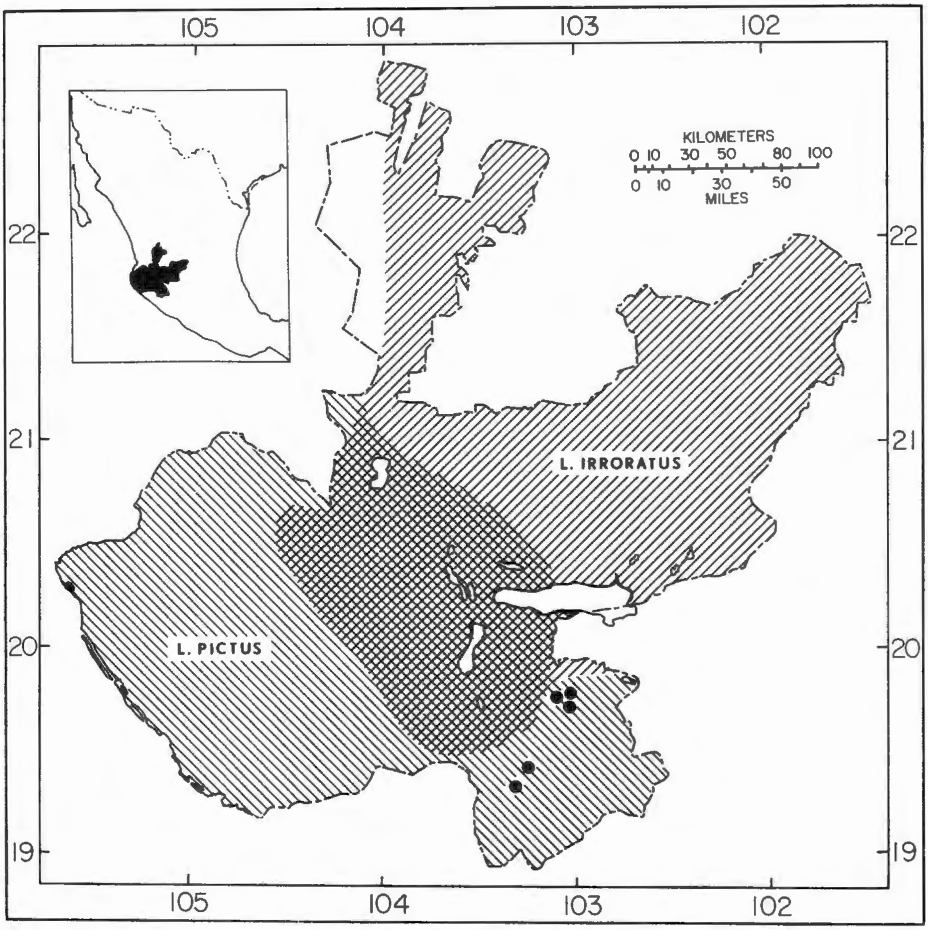


FIG. 30.—Geographic distribution of three species of *Liomys* in Jalisco, México. Closed circles indicated areas from which *Liomys spectabilis* has been taken. The inset map in the upper, left-hand corner indicates the position of the state of Jalisco in western México.

Mean length of ear of three adult males and six adult females was, respectively, 16.3 (15.0-17.0) and 16.8 (16.0-17.5); mean weight of these animals (females not pregnant) was 68.0 (61.9-72.7) and 53.2 (47.9-65.7).

Specimens examined (21).—JALISCO: 8 km. N Contla, 4300 ft., 3 (KU); 6 km. NE Contla, 1310 m., 1 (KU); 3.3 mi. NE Contla, 3900 ft., 4 (KU); 3 mi. NE Contla, 3850 ft., 1 (KU); 2.2 mi. NE Contla, 3850 ft., 7 (KU); 8½ mi. S Mazamitla, 5300 ft., 3 (KU); 12 mi. NE Pihuamo, 3150 ft., 1 (MSU); 8 mi. SW Tecalitlán, 1 (CAS).

Marginal records.—JALISCO: 8½ mi. S Mazamitla; *6 km. NE Contla*; 12 mi. NE Pihuamo; 8 mi. SW Tecalitlán; 2.2 mi. NE Contla; 8 km. N Contla.

Liomys salvini

Salvin's Spiny Pocket Mouse

Liomys salvini is the species of the genus that occurs throughout much of the Pacific coast and slopes of the adjacent mountains of Central America. The northernmost record is Reforma, Oaxaca, from where the species occurs southward through Chiapas, Guatemala, El Salvador, Honduras, Nicaragua, to central Costa Rica. Although *L. salvini* is mainly confined to the Pacific drainage, it does occur in the dry valleys of the Caribbean drainage of central and eastern Guatemala; evidently the species occurs along the dry valley of the Río Motagua and its tributaries as far as San Pedro Sula in northern Honduras. The southernmost record for the species is from Monte Rey, 22 kilometers south of San José, Costa Rica.

Diagnosis

External and cranial measurements small for the genus, tail being especially short; protoloph of permanent upper premolar appears to be composed of one cusp, metaloph composed of three and sometimes four cusps, metacone of metaloph sometimes larger than hypocone, entostyle distinctly separated from other cusps of metaloph; re-entrant angle on labial margin of lower premolar connected with median valley; baculum with large rounded base, shaft oval to point just posterior to the slightly upturned tip where it is dorsoventrally flattened; glans penis medium-sized in comparison with length of baculum, tip of glans short; glans highly sculptured, ventral folds deeply incised; urethral lappets bilobed; 2N = 56; FN = 86; head of spermatozoon short with bluntly rounded apex, distinct neck between head and midpiece; wings of pterygoids narrow; parasitized by the anopluran, *Fahrenholzia fairchildi*; six plantar tubercles; upper parts grayish brown to deep chocolate brown; no lateral stripe; underparts white; hairs on back curled so as to be conspicuous above spines.

Comparisons

Specimens of *Liomys salvini* are easily distinguished from those of *Liomys adspersus* by their much smaller measurements for all external and cranial characters (except for interparietal width, which averages broader in *salvini*). The morphology of the bacula and glandes of these two species is similar; however, the glans of *salvini* is somewhat longer in comparison with length of the baculum than in *adspersus*. Both species have 56 chromosomes, but *salvini* has at least one more pair of metacentric chromosomes (FN = 86 in *salvini* and 84 or less in *adspersus*). The structure of the head and neck of the spermatozoon of *salvini* resembles that of *adspersus*, but the head of the sperm of *salvini* is significantly broader than that of *adspersus* and the neck between the head and the midpiece is significantly longer in *adspersus* than in *salvini*.

For comparisons with *Liomys irroratus*, *Liomys pictus*, and *Liomys spectabilis*, see accounts of those species.

Ecology

The major part of the geographic range of *Liomys salvini* is in the dry tropical lowland forests of the Pacific coast of Oaxaca, Chiapas, and Central America. The species also occurs rather extensively along the Pacific slopes of the mountains of Central America, reaching an altitude of about 5000 feet around Guatemala City and 4000 feet in the vicinity of San José, Costa Rica. The only region in the Caribbean drainage in which *Liomys salvini* is common is in the dry habitat along the Río Motagua and Río Negro in Guatemala and extreme northwestern Honduras.

Some field observations on *Liomys salvini* can be found in Goodwin's reports on the mammals of Guatemala (1934:32-35) and Costa Rica (1946:375) and in Villa's account of the mammals of the department of Soconusco, Chiapas (1949). Described briefly below are 10 localities from which specimens of *Liomys salvini* have been collected. Of these, seven are in Nicaragua because extensive ecological data are available for material from there and because of my own first-hand knowledge of the country gained during two field seasons under a contract (DA-49-193-MD-2215) to J. Knox Jones, Jr., from the Army Research and Development Command.

16 km. SW Tapachula, 35 m., Chiapas.—This place is located on the flat coastal plain south of Tapachula, which is presently under extensive cultivation for cotton. The author with a field party of four other persons from The University of Kansas collected mammals here from 14 to 17 July 1969. Some specimens of *Liomys salvini* were obtained under large, buttress-rooted trees along the bank of a small stream. The traps were set there in holes at the bases of trees, around rotting stumps, and along fallen logs; the ground cover was sparse, probably because of shade from the tall trees. Specimens of Salvin's spiny pocket mouse were also obtained in an area of tall dense grass, growing between a plowed field and the road to Puerto Madero. Other small mammals obtained in this area were *Oryzomys palustris, Tylomys nudicaudus, Reithrodomtomys gracilis, Peromyscus gymnotis, Baiomys musculus,* and *Sigmodon hispidus.*

Km. 24 on highway S Guatemala City, 4100 ft., Guatemala, Guatemala.—This locality, which is located along the Pacific slope of the Guatemalan highlands, was visited on 29 February and 1 March 1960, by E. S. Booth and a field party. Traps were set in holes along a dry stream bed and in brush and grass near the highway. Other small rodents collected here were *Reithrodontomys fulvescens, Peromyscus mexicanus, Baiomys musculus,* and *Neotoma mexicana.*

3 mi. E Jocotán, 1400 ft., Chiquimula, Guatemala.—Vegetation around a hot spring and stream at this place was relatively lush, but elsewhere in the vicinity consisted of tropical deciduous scrub. The stream from the spring flows into the Río Motagua to the northwest of Jocotán. Traps were set in a variety of habitats, including a rocky outcrop near the spring, matted grass and cane, and among the trees near the stream. In addition to *Liomys salvini, Oryzomys palustris, Ototylomys phyllotis,* and *Sigmodon hispidus* were obtained.

4 1/2 km. N Cosigüina, 15 m., Chinandega, Nicaragua.—This place is located on the Cosigüina Peninsula in northwestern Nicaragua. Most of the peninsula is low and relatively flat surrounding Volcán de Cosigüina, which rises to a height of 807 meters. The vegetation in most places is tropical deciduous scrub, which is so dense that it is nearly impenetratable in uncleared areas. At the time of year that we visited the peninsula, 1 March through 6 March 1968, much of the woody vegetation was leafless and the overall appearance of the area was that of extreme aridity. At 4½ kilometers north of Cosigüina a warm spring forms a marshy area, which is surrounded by relatively lush vegetation. Specimens of *Liomys salvini* were obtained around piles of brush and felled trees near the spring. Specimens of

Oryzomys fulvescens, O. palustris, and *Sigmodon hispidus* were trapped around the marsh and several *Sciurus variegatoides* were shot from large trees in the area.

Hacienda Bellavista, 720 m., Volcán Casita, Chinandega, Nicaragua.—Volcán Casita is one of the isolated volcanos rising from the low, flat coastal plain of northwestern Nicaragua. Hacienda Bellavista is located on the southwestern slope of the volcano, slightly more than half way to the top. Deciduous forest was present in the vicinity of the hacienda headquarters but pines grew at higher elevations. Much of the understory had been cleared and coffee planted under the tall trees; the road leading to the hacienda was lined by dense low shrubs and vines. Trapping was done in the coffee plantings, along the road, on rocky slopes, and along rock fences. Other small mammals obtained at this place in addition to Salvin's spiny pocket mouse were *Marmosa mexicana, Caluromys derbianus, Sciurus variegatoides, Ototylomys phyllotis, Nyctomys sumichrasti, Peromyscus mexicanus,* and *Sigmodon hispidus.*

1 km. NE Esquipulas, 420 m., Matagalpa, Nicaragua.—At this locality a large stream, lined with some large deciduous trees (including at least one species of fig), runs through an area of low tropical deciduous scrub. *Liomys salvini* was abundant in this area (20 specimens), being taken in traplines placed among rocks along the stream bank, along a rock fence adjacent to an area of tall grass, and in the scrub forest. The only other small rodents trapped in this area were *Oryzomys palustris,* taken along the stream bank. At a nearby locality, but much higher altitude (La Danta, 1 km. N, 5 km. E Esquipulas, 780 m.) where the vegetation was lusher and the climate much cooloer, only two specimens of *Liomys salvini* were obtained (in a grassy area). Three specimens of *Heteromys desmarestianus* were collected at a third locality in this vicinity—at a still higher elevation (2 km. N, 6 km. E Esquipulas, 960 m.)—but but no specimens of *Liomys salvini* were obtained here.

1 km. N, 2 1/2 km. W Villa Somoza, 330 m., Chontales, Nicaragua.—Villa Somoza is located in the Caribbean drainage of Nicaragua and is one of the few places south of Guatemala from which *Liomys salvini* has been collected in this drainage. Most of the area has been cleared and supports tall lush grass used for grazing. Only along a small stream did large trees remain. Traps were placed along the stream, at the bases of large trees, and in the areas of grass, but with only limited trapping success. Small mammals obtained in this area include *Liomys salvini, Oryzomys fulvescens,* and *Ototylomys phyllotis.*

3 km. N, 4 km. W Diriamba, 600 m., Carazo, Nicaragua.—This locality is situated atop the Meseta de los Pueblos. At the times we visited the area (August 1967 and April 1968) it had the appearance of being relatively dry; the large trees, many more than 150 feet tall, gave the area a much different appearance from the scrub forest elsewhere in western Nicaragua. Coffee and bananas were planted under the large trees. I had the most success collecting *Liomys* among logs and mounds of dirt that had been cleared from a large area so that bananas could be planted. There was no ground cover in the area except the logs and traps were set at various intervals along these piles. Other small mammals obtained at this place included *Didelphis marsupialis, Caluromys derbianus, Sciurus variegatoides, Oryzomys fulvescens, Peromyscus mexicanus,* and *Coendou mexicanus.*

4 km. S, 1 1/2 km. E Alta Gracia, 40 m., Isla de Ometepe, Rivas, Nicaragua.—Alta Gracia is located on the island of Ometepe in Lake Nicaragua about 30 kilometers northeast of Rivas and 60 kilometers west of El Morrito. The vegetation on the island is deciduous tropical forest similar to that of the adjacent western coast of Nicaragua. The general area in which we trapped was highly agriculturized with cornfields, banana plantations, and overgrazed pastures. The specimens of *Liomys salvini* were taken in traps set in an abandoned cornfield that was overgrown with weeds and along a rock fence at the end of this field. I caught 11 specimens of *salvini* in this field in 60 snap-traps, but no other small rodents were obtained. A short distance away was a small stream along which was a marshy area with tall grass and weeds. Specimens of *Oryzomys fulvescens* and *O. palustris* were trapped along this stream, but no specimens of Salvin's spiny pocket mouse were obtained there.

Río Javillo, 3 km. N, 4 km. W Sapoá, 40 m., Rivas, Nicaragua.—At this place tall trees were found for about 40 meters on either side of the Río Javillo, but beyond this area was

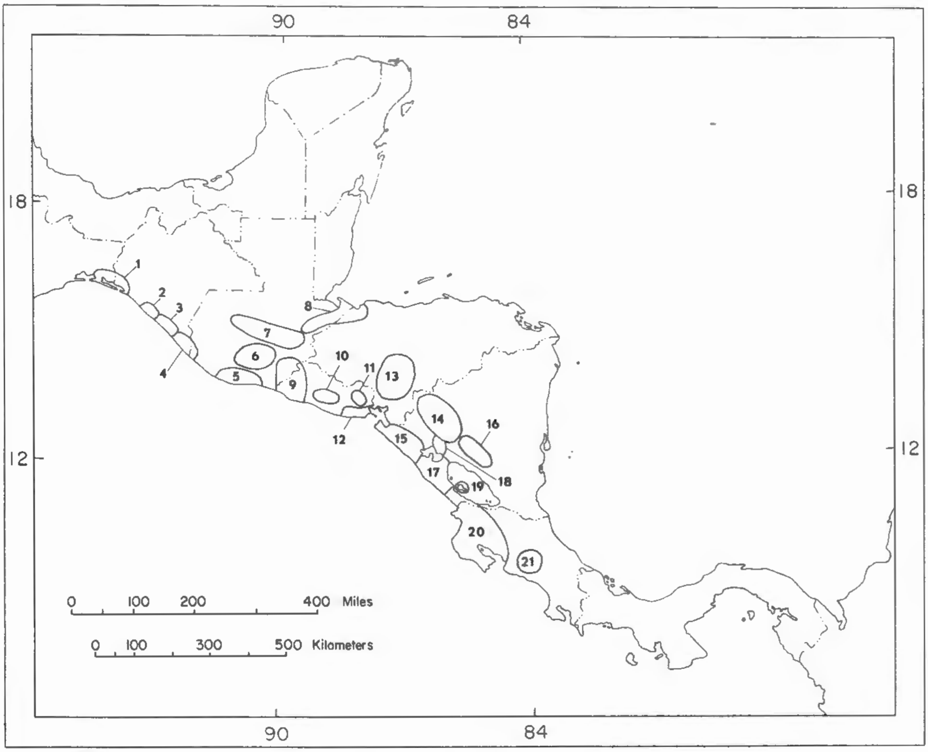


FIG. 31.—Approximate geographic areas included in the 21 samples of *Liomys salvini*. See text for localities included in each sample.

shorter deciduous tropical forest common in the lowlands of western Nicaragua. Traps were placed around the bases of the trees and along the banks of the stream. In addition to specimens of *Liomys salvini* the following small rodents were obtained along the Río Javillo: *Oryzomys palustris*, *Reithrodontomys gracilis*, *Ototylomys phyllotis*, and *Peromyscus mexicanus*.

GEOGRAPHIC VARIATION

Univariate Analysis

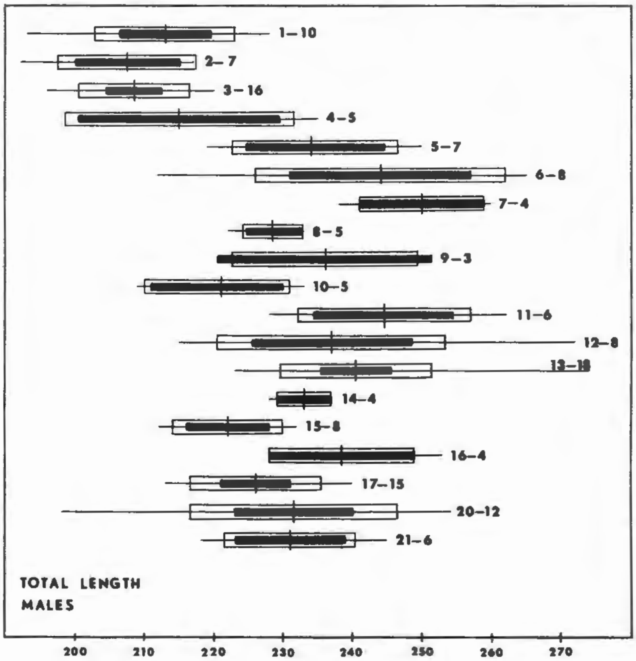
Nearly all adult specimens from throughout the geographic range of *Liomys salvini* were grouped into 20 samples for males and 21 samples for females as follows (Fig. 31): *sample 1*—OAXACA (Reforma) and CHIAPAS (Tonalá); *sample 2*—CHIAPAS (Pijijiapan); *sample 3*—CHIAPAS (Escuintla, Mapastepec); *sample 4*—CHIAPAS (Huehuetán, Puerto Madero, Tapachula) and GUATEMALA (Hda. California); *sample 5*—GUATEMALA (Astillero, Concepción del Mar, Finca Valle-Lirios, Iztapa, Masagua, San José); *sample 6*—GUATEMALA (Dueñas, Guatemala, Lake Amatitlán); *sample 7*—GUATEMALA (El Rancho, Granados, Progreso, Rabinal, Sacapulas, Salamá); *sample 8*—GUATEMALA (Cabañas, Gualán, 152 km. NE Guatemals City) and HONDURAS (San Pedro Sula); *sample 9*—GUATEMALA (Cerro las Flores, Lake Atescatempa, Monogoy, San Cristóbal) and EL

SALVADOR (El Tablón, Lake Coatepeque, Hda. Chilata); *sample 10*—EL SALVADOR (Los Planes, San Salvador, Santa Tecla); *sample 11*—EL SALVADOR (Divisadero, Mt. Cacaguatique, Monte Cristo Mine); *sample 12*—EL SALVADOR (Lake Olomega, Pine Peak, Puerto del Triunfo, Río Goascorán, Río San Miguel, Volcán San Miguel); *sample 13*—HONDURAS (Cerro de los Cuches, El Caliche Orica, Escuela Agricultura Panamericana, La Cueva Archaga, La Flor Archaga, La Piedra de Jesús, La Venta, Monte Redondo); *sample 14*—NICARAGUA (Condega, Darailí, Esquipulas, Estelí, Uluse); *sample 15*—NICARAGUA (Cosigüina, Hda. Bellavista, Puerto Momotombo, San Antonio, Tamarindo, Volcán Chinandega); *sample 16*—NICARAGUA (Santa Rosa, Villa Somoza); *sample 17*—NICARAGUA (Diriamba, El Crucero, Hda. Azacualpa, La Calera, Managua, Sabana Grande, San Pablo); *sample 18*—NICARAGUA (Dario, Las Maderas—this sample contains only females); *sample 19*—NICARAGUA (Alta Gracia, Mérida, Moyogalpa); *sample 20*—NICARAGUA (Finca Amayo, Rivas) and COSTA RICA (Bagaces, Boca del Barranca, Cerro San Juan, Esparta, Filadelfia, Finca Jiménez, Liberia, Playa del Coco, San Francisco Esparta, Tempate); *sample 21*—COSTA RICA (Altos Escazú, Cañas, Cangrejal, Los Higuerones, Monte Rey, Sabinilla de Pirrís, San Ignacio, Santa Ana, Villa Colón).

Included in the above group of samples are specimens that have formerly been known under the names *Liomys anthonyi*, *Liomys crispus*, and *Liomys heterothrix* as well as individuals previously referred to *Liomys salvini*. Reasons for inclusion of these taxa under a single name will be discussed in the following sections. Dice grams have been prepared for four measurements (Fig. 32) to facilitate demonstration of trends in geographic variation. Table 21 gives standard statistics for samples of *Liomys salvini*.

External Measurements

Specimens from coastal Oaxaca, Chiapas, and southwestern Guatemala (samples 1-4) have the shortest mean total length for the species (Fig. 32 and Tables 21, 22). Males from the southern coast of Guatemala (sample 5) have a mean total length that is similar to that of specimens from the vicinity of Guatemala City (sample 6), whereas females from sample 5 have a mean value intermediate between those of specimens from coastal Chiapas and southwestern Guatemala (sample 4) and sample 6. A series of samples, with one exception, from Guatemala City, Río Motagua, Río Negro in Guatemala, El Salvador, Honduras, and north-central Nicaragua (6-14) are characterized by mice with a total length averaging nearly 230 or more. The one exception is specimens from the vicinity of San Salvador, El Salvador (sample 10), which have a total length that is shorter (221.0 for males, 221.8 for females) than would be expected at this place. The largest individuals in this group of samples are from the vicinity of Sacapulas and Salamá, Guatemala (sample 7), northwestern El Salvador (11), and Honduras (13). Specimens from coastal western Nicaragua (15) and the Meseta de los Pueblos south of Managua (17) have mean total lengths that are intermediate for the species. However, males from sample 17 approach the values for specimens to the north (14). Females from sample 18 have a mean total length that more nearly



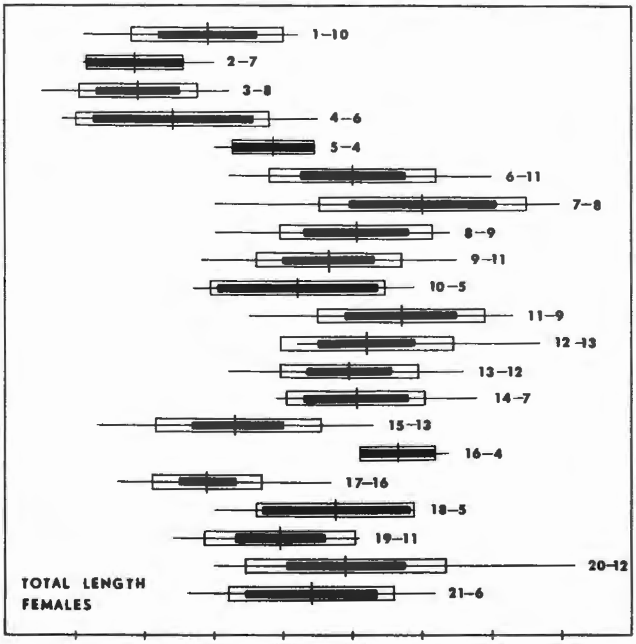
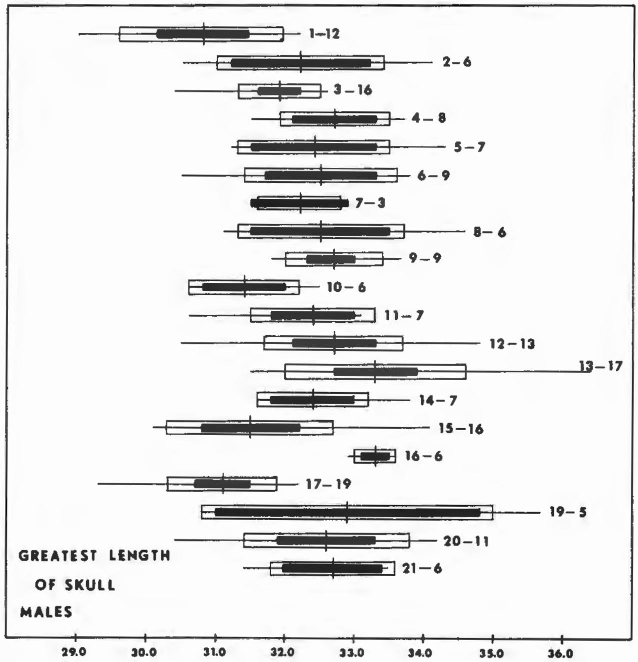


FIG. 32.—Dice grams for four selected measurements of males and females of *Liomys salvini*. See Fig. 9 for method used in constructing these grams. See Fig. 31 and text for key to samples.



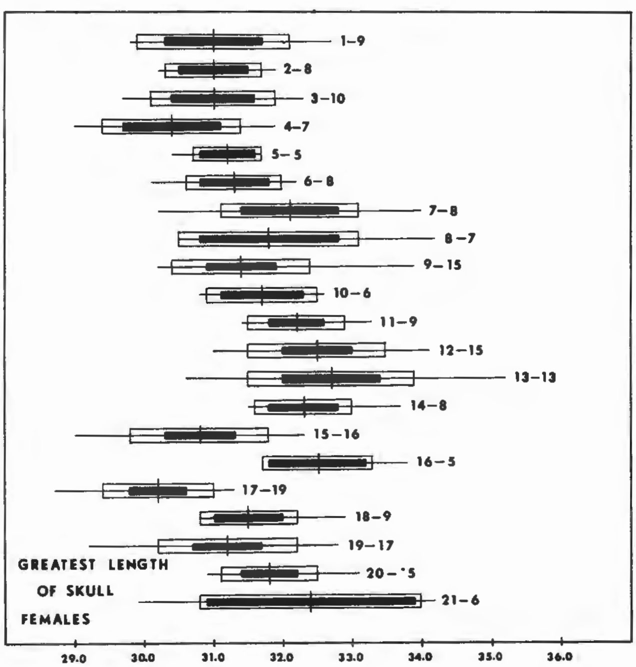
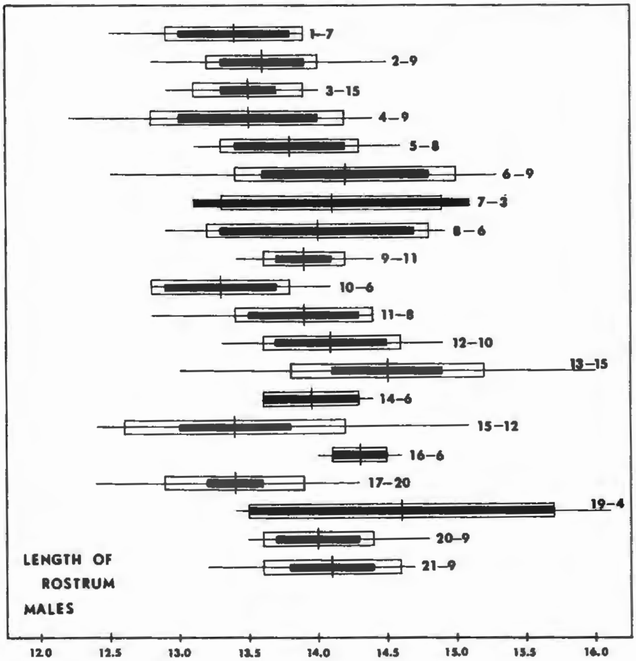


FIG. 32.—Continued.



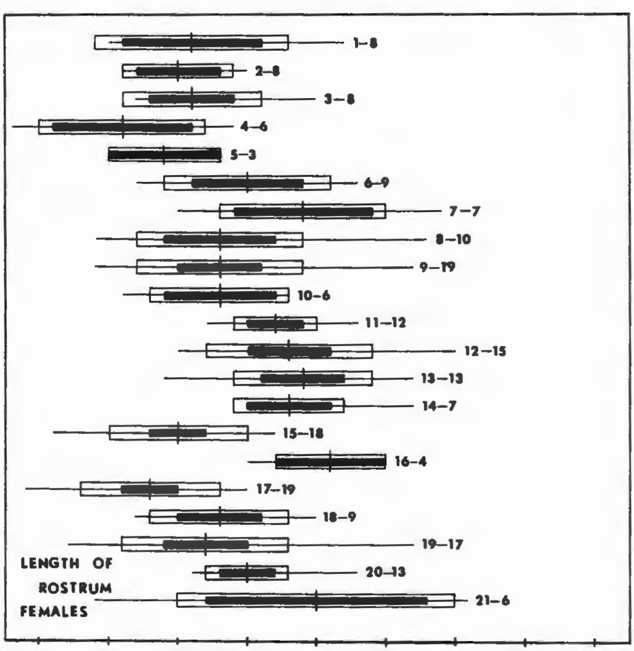
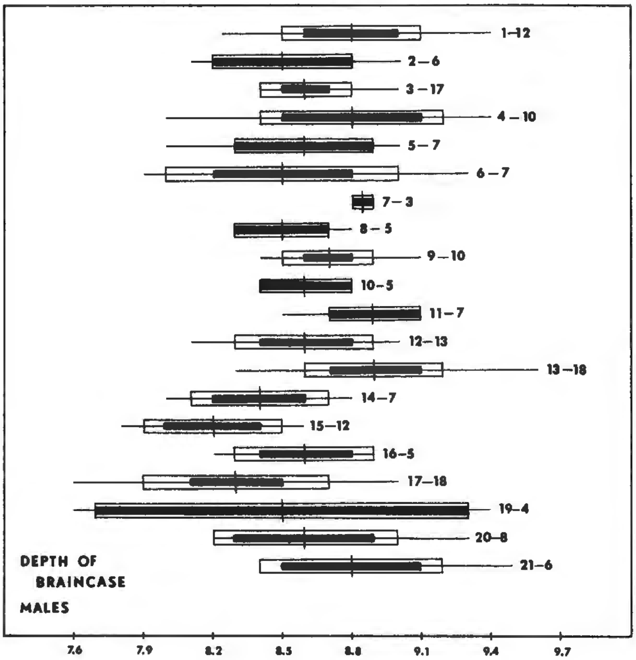


FIG. 32.—Continued.



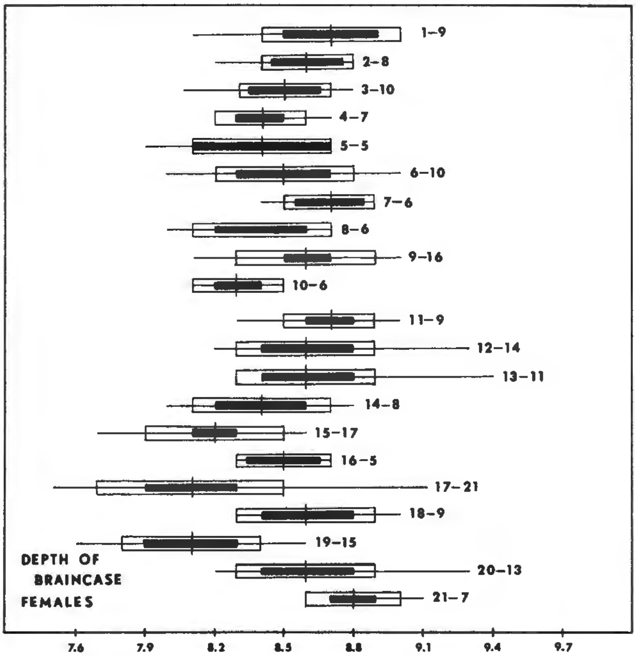


FIG. 32.—Continued.

TABLE 21.—*Geographic variation in external and cranial measurements among 21 samples of* Liomys salvini. *See text for key to sample numbers.*

	Males				Females			
Sample number	N	Mean	Range	2 SE	N	Mean	Range	2 SE
				Total length				
1	10	213.2	193.0-228.0	6.37	10	209.2	191.0-222.0	7.00
2	7	207.6	192.0-217.0	7.42	7	198.3	191.0-210.0	5.46
3	16	208.5	196.0-220.0	4.07	8	198.8	185.0-212.0	6.16
4	5	215.0	202.0-235.0	14.78	6	204.2	188.0-225.0	11.33
5	7	234.4	219.0-250.0	9.04	4	218.5	210.0-223.0	5.92
6	8	244.0	212.0-265.0	12.86	11	229.8	212.0-250.0	7.36
7	4	250.3	238.0-260.0	9.18	8	239.8	210.0-260.0	10.59
8	5	228.4	222.0-233.0	4.22	9	230.4	210.0-244.0	7.27
9	3	236.3	225.0-251.0	15.38	11	226.6	208.0-245.0	6.34
10	5	221.0	209.0-233.0	9.94	5	221.8	207.0-239.0	11.34
11	6	244.3	228.0-262.0	10.19	9	237.0	215.0-253.0	8.01
12	8	237.1	215.0-272.0	11.74	13	232.0	222.0-257.0	6.82
13	18	240.3	223.0-269.0	5.16	12	229.3	212.0-246.0	5.75
14	4	233.0	228.0-237.0	4.24	7	230.4	219.0-248.0	7.69
15	8	222.1	212.0-232.0	5.90	13	213.5	193.0-233.0	6.55
16	4	238.3	229.0-253.0	10.69	4	236.5	232.0-244.0	5.74
17	15	226.1	213.0-240.0	4.92	16	209.1	196.0-227.0	4.05
18					5	227.4	210.0-239.0	10.40
19	3	241.7	209.0-262.0	33.00	11	219.7	204.0-231.0	6.64
20	12	231.7	198.0-254.0	8.60	12	228.9	210.0-262.0	8.51
21	6	230.8	218.0-245.0	7.94	6	223.8	206.0-242.0	9.63
				Length of tail				
1	10	105.3	98.0-114.0	4.01	10	104.1	95.0-115.0	4.54
2	7	100.3	94.0-112.0	4.63	7	93.4	87.0-101.0	3.97
3	16	101.4	88.0-112.0	3.15	8	93.0	81.0-102.0	4.60
4	5	97.0	90.0-110.0	7.24	6	95.3	85.0-110.0	7.99
5	7	115.9	104.0-128.0	6.96	4	104.3	102.0-108.0	2.87
6	8	126.1	111.0-145.0	7.70	11	121.0	108.0-132.0	4.44
7	4	124.8	116.0-135.0	8.81	8	126.9	110.0-136.0	6.66
8	5	114.6	108.0-126.0	6.62	9	118.1	102.0-132.0	5.39
9	3	115.7	98.0-131.0	19.19	11	115.2	108.0-129.0	4.42
10	5	106.2	98.0-118.0	8.86	5	112.8	104.0-127.0	8.66
11	7	124.4	117.0-125.0	6.08	9	120.0	114.0-128.0	3.28
12	9	118.3	104.0-134.0	5.46	13	118.0	102.0-132.0	5.11
13	18	123.1	105.0-143.0	4.62	12	122.1	110.0-135.0	4.87
14	4	118.5	108.0-128.0	8.19	7	117.4	110.0-128.0	5.54
15	8	108.9	99.0-119.0	4.93	13	108.1	95.0-128.0	5.29
16	4	115.5	111.0-120.0	3.87	4	118.8	112.0-124.0	4.99
17	15	113.3	94.0-124.0	3.85	16	107.3	100.0-121.0	2.92
18					5	123.8	104.0-155.0	11.36
19	3	116.0	104.0-123.0	12.06	11	110.6	103.0-119.0	2.88
20	12	115.2	107.0-130.0	3.57	12	117.5	104.0-129.0	4.58
21	5	114.2	112.0-116.0	1.60	5	116.2	105.0-132.0	9.02

TABLE 21.—*Continued*

				Length of hind foot				
1	12	27.3	25.5-29.0	0.60	10	27.2	26.5-29.0	0.42
2	9	27.4	26.0-29.0	0.75	8	26.4	25.0-27.0	0.65
3	17	26.9	25.0-28.0	0.44	10	26.0	24.0-27.0	0.60
4	6	27.3	25.0-30.0	1.43	6	26.7	25.0-29.0	1.12
5	8	27.9	26.0-29.0	0.80	5	26.6	25.0-28.0	1.02
6	8	29.0	27.0-30.0	0.76	12	27.8	23.0-30.0	1.08
7	4	28.5	27.0-30.0	1.73	8	28.8	26.0-32.0	1.46
8	4	28.8	28.0-31.0	1.50	9	27.2	25.0-28.0	0.73
9	4	27.6	26.0-30.0	1.70	12	27.0	25.0-29.0	0.74
10	5	27.6	27.0-28.0	0.49	6	27.7	26.0-29.0	0.99
11	8	28.0	26.0-30.0	0.93	10	27.7	27.0-29.0	0.52
12	13	27.8	26.0-29.0	0.56	15	27.9	26.0-31.0	0.64
13	19	26.4	23.0-30.0	0.83	14	26.7	22.0-30.0	1.06
14	6	28.5	27.0-30.0	0.86	8	27.3	26.0-29.0	0.73
15	12	26.8	25.0-30.0	0.86	10	26.4	24.0-28.0	0.90
16	6	28.8	28.0-30.0	0.80	5	28.6	28.0-29.0	0.49
17	15	27.1	25.0-30.0	0.69	21	26.0	24.0-29.0	0.46
18					5	25.4	24.0-28.0	1.50
19	3	28.7	28.0-29.0	0.67	17	27.5	26.0-30.0	0.55
20	12	27.5	25.0-30.0	0.92	12	26.3	25.0-28.0	0.61
21	7	27.6	25.0-30.0	1.44	6	26.3	25.0-29.0	1.33
				Greatest length of skull				
1	12	30.8	29.0-32.2	0.67	9	31.0	29.8-32.7	0.73
2	6	32.2	30.5-34.1	0.98	8	31.0	30.2-31.9	0.48
3	16	31.9	30.4-32.6	0.32	10	31.0	29.7-32.3	0.58
4	8	32.7	31.5-33.7	0.59	7	30.4	29.0-31.9	0.73
5	7	32.4	31.2-34.3	0.86	5	31.2	30.4-31.7	0.45
6	9	32.5	30.5-33.8	0.75	8	31.3	30.1-32.2	0.50
7	3	32.2	31.5-32.5	0.67	8	32.1	31.0-34.0	0.68
8	6	32.5	31.1-34.6	0.96	7	31.8	30.5-34.2	1.00
9	9	32.7	31.8-33.7	0.45	15	31.4	30.2-33.9	0.50
10	6	31.4	30.6-32.5	0.64	6	31.7	30.8-32.6	0.62
11	7	32.4	30.6-33.1	0.65	9	32.2	31.4-33.3	0.43
12	13	32.7	30.5-34.8	0.57	15	32.5	31.0-34.1	0.50
13	17	33.3	31.5-36.4	0.63	13	32.7	30.6-35.2	0.66
14	7	32.4	31.6-33.8	0.58	8	32.3	31.5-33.7	0.53
15	12	31.5	30.1-34.1	0.69	16	30.8	29.0-32.3	0.47
16	6	33.3	32.9-33.6	0.22	5	32.5	31.8-33.8	0.70
17	19	31.1	29.3-32.2	0.36	19	30.2	28.7-31.3	0.37
18					9	31.5	30.8-32.9	0.45
19	5	32.9	30.8-35.7	1.85	17	31.2	29.2-32.8	0.48
20	11	32.6	30.4-34.2	0.70	15	31.8	30.9-33.1	0.36
21	6	32.7	31.4-33.5	0.70	6	32.4	29.8-34.2	1.33
				Zygomatic breadth				
1	5	14.4	13.9-15.0	0.38	6	14.5	13.9-15.2	0.44
2	7	14.8	14.3-15.7	0.39	7	14.6	14.3-15.1	0.20
3	11	14.9	14.3-15.2	0.19	7	14.6	13.8-15.4	0.40
4	7	15.2	14.2-16.0	0.56	6	14.8	13.8-15.9	0.72

TABLE 21.—*Continued*

5	5	14.9	14.3-15.4	0.41	5	14.9	14.3-15.3	0.33
6	7	15.1	14.4-15.7	0.33	6	14.9	14.4-15.2	0.23
7	2	15.0	14.6-15.3	0.70	4	14.8	14.0-15.4	0.58
8	2	15.2	14.0-16.4	2.40	3	15.1	14.5-16.0	0.92
9	10	14.7	13.8-15.8	0.37	13	14.7	13.8-15.8	0.31
10	5	14.5	14.2-14.8	0.25	6	14.7	14.1-15.1	0.31
11	5	14.9	14.4-15.3	0.30	12	15.0	14.6-15.6	0.20
12	10	15.2	14.7-15.6	0.22	10	15.1	14.7-15.8	0.29
13	3	15.6	15.1-16.6	0.97	4	15.4	15.1-15.6	0.22
14	5	14.6	13.8-14.9	0.39	6	14.8	14.4-15.1	0.23
15	7	14.7	14.0-15.3	0.38	12	14.5	13.6-15.3	0.23
16	2	15.1	15.0-15.2	0.20	4	14.9	14.7-15.3	0.29
17	14	14.4	13.5-15.7	0.34	15	13.9	13.0-14.8	0.24
18					8	14.3	13.9-14.8	0.23
19	4	14.9	13.8-15.3	0.70	12	14.7	14.2-15.3	0.22
20	2	15.4	14.8-15.9	1.10	9	14.8	13.8-15.9	0.42
21	4	15.1	14.9-15.6	0.34	2	15.3	14.9-15.6	0.70
				Interorbital constriction				
1	12	6.5	6.3-6.9	0.10	10	6.4	6.0-6.9	0.19
2	9	6.4	6.1-6.7	0.14	8	6.5	6.2-6.9	0.14
3	18	6.4	5.9-6.9	0.11	10	6.5	6.2-6.8	0.10
4	12	6.5	6.0-7.0	0.19	10	6.4	6.1-6.8	0.13
5	8	6.5	6.0-6.7	0.16	5	6.6	6.3-7.0	0.25
6	9	7.0	6.4-7.3	0.20	10	6.6	6.0-7.1	0.22
7	3	6.6	6.2-6.8	0.37	8	6.7	6.2-7.3	0.29
8	8	7.0	6.5-7.5	0.22	11	6.7	6.4-7.0	0.13
9	12	6.8	6.3-7.0	0.11	18	6.7	6.4-7.3	0.14
10	6	6.8	6.5-7.3	0.23	6	6.7	6.6-6.9	0.08
11	8	7.0	6.6-7.4	0.19	12	6.7	6.2-7.5	0.23
12	13	6.7	6.1-7.0	0.17	16	6.8	6.3-7.4	0.15
13	20	6.9	6.4-7.6	0.15	17	6.9	6.4-7.8	0.18
14	7	6.7	6.4-7.0	0.18	9	6.8	6.3-7.3	0.20
15	12	6.8	6.3-7.5	0.20	19	6.7	6.0-7.1	0.11
16	6	6.8	6.5-7.0	0.17	5	6.7	6.5-7.0	0.19
17	20	6.7	6.2-7.4	0.13	23	6.5	6.1-6.8	0.07
18					9	6.9	6.4-7.5	0.24
19	5	7.0	6.2-8.0	0.59	18	6.5	6.0-7.0	0.12
20	13	6.8	6.2-7.4	0.25	15	6.9	6.5-7.5	0.14
21	8	7.0	6.6-7.7	0.28	7	7.2	6.8-7.6	0.23
				Mastoid breadth				
1	12	13.6	12.8-14.1	0.24	9	13.7	13.3-14.5	0.25
2	6	13.8	13.2-14.6	0.46	8	13.8	13.5-14.1	0.15
3	17	13.8	13.2-14.4	0.14	10	13.7	13.4-14.2	0.17
4	12	13.9	13.2-15.0	0.30	10	13.7	13.1-14.5	0.33
5	7	14.1	13.4-15.1	0.42	5	14.0	13.2-14.5	0.44
6	7	13.9	13.1-14.7	0.36	9	13.7	13.4-14.0	0.15
7	3	13.8	13.5-14.0	0.31	8	13.9	13.3-14.5	0.29
8	6	14.0	13.3-14.5	0.36	9	13.9	13.3-14.4	0.24
9	11	14.0	13.3-14.6	0.22	15	13.8	13.1-14.5	0.18
10	5	13.7	13.4-13.9	0.17	16	13.8	13.4-14.5	0.34

TABLE 21.—*Continued*

11	7	14.3	14.0-14.7	0.20	11	14.1	13.6-14.7	0.21
12	13	14.3	13.9-14.7	0.14	15	14.3	13.5-15.1	0.19
13	20	14.2	13.3-15.0	0.20	14	14.0	13.4-14.9	0.24
14	7	13.7	13.3-14.1	0.23	9	13.9	13.2-14.3	0.22
15	12	14.0	13.1-14.8	0.30	19	13.7	13.3-14.2	0.14
16	6	14.2	14.0-14.7	0.20	5	14.2	13.8-14.9	0.43
17	19	13.5	12.9-14.2	0.16	23	13.3	12.7-14.2	0.17
18					9	13.6	13.3-14.0	0.18
19	5	13.9	13.0-14.6	0.60	17	13.4	12.7-13.9	0.16
20	11	13.9	13.2-14.5	0.22	13	13.9	13.0-14.5	0.25
21	6	13.7	13.3-14.3	0.31	7	13.8	13.4-14.0	0.16
				Length of nasals				
1	12	11.4	10.4-12.5	0.43	10	11.4	10.9-12.0	0.25
2	9	11.9	11.1-13.2	0.40	8	11.6	10.9-12.4	0.36
3	15	12.2	11.4-12.7	0.25	9	11.7	10.8-12.2	0.30
4	10	11.9	10.8-12.8	0.47	9	11.5	10.2-12.8	0.06
5	8	12.4	11.5-13.3	0.43	5	11.6	11.1-12.3	0.52
6	9	12.4	11.0-13.2	0.49	9	11.9	11.0-12.6	0.37
7	4	12.7	12.0-13.5	0.69	8	12.3	11.6-13.1	0.41
8	8	12.7	11.3-14.2	0.76	11	11.7	11.2-12.4	0.21
9	11	12.4	11.7-13.6	0.32	19	11.9	11.0-13.8	0.34
10	6	11.8	10.8-12.7	0.51	6	11.7	10.7-13.0	0.67
11	8	12.4	11.5-13.1	0.41	12	12.2	11.6-13.2	0.30
12	13	12.8	11.1-14.3	0.46	16	12.5	11.5-13.2	0.31
13	19	13.0	11.2-14.4	0.41	16	12.6	11.2-13.7	0.35
14	7	12.4	11.5-13.9	0.73	9	12.2	11.6-12.8	0.31
15	12	12.0	10.6-13.3	0.43	18	11.7	10.6-12.9	0.26
16	6	12.8	12.5-13.3	0.28	5	12.3	11.7-13.3	0.57
17	20	11.9	11.0-12.8	0.21	21	11.5	10.4-12.2	0.23
18					9	11.8	11.2-12.5	0.35
19	5	13.1	11.8-14.3	1.07	19	12.0	10.9-13.0	0.24
20	11	12.5	11.7-13.4	0.41	15	12.2	11.4-13.2	0.30
21	9	13.0	12.0-13.5	0.31	6	12.9	11.0-14.1	0.90
				Length of rostrum				
1	7	13.4	12.5-13.9	0.40	8	13.1	12.5-14.2	0.48
2	9	13.6	12.8-14.5	0.29	8	13.0	12.6-13.5	0.28
3	15	13.5	12.9-14.0	0.18	8	13.1	12.7-14.0	0.32
4	9	13.5	12.2-14.4	0.47	6	12.6	11.8-13.4	0.51
5	8	13.8	13.1-14.6	0.37	3	12.9	12.5-13.2	0.41
6	9	14.2	12.5-15.3	0.59	9	13.5	12.7-14.3	0.37
7	3	14.1	13.3-15.0	0.98	7	13.9	13.0-14.9	0.48
8	6	14.0	12.9-14.9	0.66	10	13.3	12.4-14.8	0.43
9	11	13.9	13.4-14.4	0.18	19	13.3	12.4-14.7	0.28
10	6	13.3	12.8-14.1	0.39	6	13.3	12.6-13.8	0.37
11	8	13.9	12.8-14.4	0.36	12	13.7	13.2-14.3	0.20
12	10	14.1	13.3-14.9	0.36	15	13.8	13.0-15.0	0.28
13	15	14.5	13.0-16.0	0.37	13	13.9	12.9-14.7	0.26
14	6	13.9	13.6-14.4	0.26	7	13.8	13.5-14.7	0.32
15	12	13.4	12.4-15.1	0.44	18	13.0	12.1-13.7	0.22
16	6	14.3	14.0-14.6	0.17	4	14.1	13.5-14.5	0.43

TABLE 21.—*Continued*

17	20	13.4	12.4-14.3	0.23	19	12.8	11.9-13.5	0.21
18					9	13.3	12.7-14.0	0.30
19	4	14.6	13.4-16.1	1.14	17	13.2	12.2-14.7	0.28
20	9	14.0	13.5-14.8	0.27	13	13.5	13.1-14.3	0.18
21	9	14.1	13.2-14.7	0.35	6	14.0	12.4-15.1	0.82
				Length of maxillary toothrow				
1	12	4.7	4.4-5.0	0.12	10	4.7	4.4-4.9	0.11
2	9	4.7	4.5-5.0	0.11	8	4.8	4.5-5.1	0.16
3	17	4.8	4.3-5.0	0.09	7	4.8	4.7-5.0	0.08
4	11	4.9	4.5-5.2	0.13	8	4.8	4.4-5.2	0.20
5	8	5.0	4.7-5.3	0.16	5	5.0	4.8-5.1	0.10
6	9	4.8	4.5-5.4	0.20	11	4.7	4.3-5.3	0.15
7	4	5.0	4.7-5.3	0.28	6	4.8	4.6-5.2	0.21
8	8	4.8	4.2-5.1	0.20	12	4.9	4.6-5.1	0.09
9	13	4.8	4.5-5.2	0.12	20	4.9	4.5-5.3	0.09
10	6	4.7	4.4-4.9	0.14	6	4.8	4.6-5.0	0.14
11	8	4.8	4.6-5.0	0.12	12	4.9	4.6-5.1	0.10
12	13	4.9	4.3-5.2	0.14	16	5.0	4.6-5.3	0.10
13	21	5.1	4.6-5.4	0.09	16	5.1	4.8-5.4	0.09
14	7	4.9	4.8-5.1	0.08	10	4.9	4.7-5.2	0.11
15	11	4.8	4.5-5.0	0.10	17	4.7	4.4-4.9	0.08
16	6	5.0	4.8-5.5	0.20	5	4.8	4.7-5.1	0.14
17	19	4.6	4.2-5.0	0.09	24	4.6	4.2-5.0	0.08
18					8	4.8	4.4-5.1	0.16
19	4	5.0	4.7-5.3	0.28	15	4.8	4.3-5.2	0.11
20	12	5.0	4.6-5.3	0.15	14	4.9	4.7-5.3	0.10
21	8	5.0	4.7-5.3	0.15	7	4.9	4.7-5.5	0.22
				Depth of braincase				
1	12	8.8	8.4-9.4	0.15	9	8.7	8.1-8.9	0.20
2	6	8.5	8.1-9.0	0.27	8	8.6	8.2-8.8	0.15
3	17	8.6	8.4-9.0	0.09	10	8.5	8.0-8.8	0.15
4	10	8.8	8.0-9.4	0.26	7	8.4	8.3-8.7	0.12
5	7	8.6	8.0-9.0	0.26	5	8.4	7.9-8.7	0.27
6	7	8.5	7.9-9.3	0.34	10	8.5	8.0-9.0	0.18
7	3	8.8	8.8-8.9	0.07	6	8.7	8.4-8.9	0.14
8	5	8.5	8.3-8.8	0.19	6	8.4	8.0-8.7	0.24
9	10	8.7	8.4-9.1	0.14	16	8.6	8.1-9.0	0.14
10	5	8.6	8.4-8.8	0.16	6	8.3	8.1-8.5	0.13
11	7	8.9	8.5-9.1	0.16	9	8.7	8.3-9.0	0.15
12	13	8.6	8.1-9.0	0.16	14	8.6	8.2-9.3	0.16
13	18	8.9	8.3-9.6	0.15	11	8.6	8.4-9.4	0.16
14	7	8.4	8.0-8.8	0.20	8	8.4	8.0-8.8	0.22
15	12	8.2	7.8-8.6	0.18	17	8.2	7.7-8.6	0.13
16	5	8.6	8.2-8.9	0.23	5	8.5	8.3-8.7	0.15
17	18	8.3	7.6-9.0	0.17	21	8.1	7.5-9.2	0.17
18					9	8.6	8.1-9.0	0.20
19	4	8.5	7.6-9.4	0.77	15	8.1	7.6-8.6	0.16
20	8	8.6	8.2-9.3	0.26	13	8.6	8.2-9.3	0.17
21	6	8.8	8.6-9.5	0.29	7	8.8	8.7-9.1	0.11

TABLE 21.—*Continued*

				Interparietal width				
1	12	8.7	8.2-9.6	0.20	9	8.8	7.8-9.5	0.37
2	6	8.9	8.6-9.2	0.22	8	8.8	8.0-9.6	0.32
3	17	8.6	7.9-9.3	0.17	10	8.8	8.2-9.8	0.31
4	11	8.7	8.0-10.0	0.33	9	8.9	8.4-10.0	0.33
5	7	9.0	8.1-9.8	0.46	5	9.5	8.6-10.1	0.54
6	8	9.1	8.2-9.9	0.47	10	8.9	8.1-9.6	0.30
7	3	9.1	8.9-9.2	0.18	7	8.8	8.0-9.8	0.51
8	5	8.9	8.2-9.4	0.48	8	8.7	8.2-9.5	0.34
9	11	8.9	7.9-9.5	0.33	16	8.9	7.9-9.9	0.27
10	6	8.6	8.0-9.2	0.32	6	8.5	7.9-9.3	0.44
11	8	9.0	8.1-9.9	0.43	10	9.0	8.1-9.4	0.29
12	13	9.0	8.2-9.7	0.23	15	9.1	8.0-9.7	0.28
13	19	9.2	8.5-10.1	0.20	14	8.7	8.2-9.3	0.19
14	7	9.0	7.2-10.5	0.81	8	8.1	7.5-9.0	0.37
15	12	8.9	8.2-9.6	0.23	18	8.7	8.0-9.3	0.17
16	6	8.7	7.7-9.6	0.58	5	8.8	8.2-9.4	0.41
17	19	8.6	7.7-9.5	0.21	22	8.7	7.6-9.8	0.20
18					9	8.8	8.0-9.4	0.36
19	5	9.0	7.8-10.0	0.75	16	8.3	7.4-8.8	
20	11	9.0	8.4-9.8	0.29	13	8.6	7.7-9.6	0.27
21	6	8.3	7.6-8.8	0.45	7	8.1	7.8-8.5	0.22
				Interparietal length				
1	12	3.9	3.5-4.4	0.16	9	4.0	3.3-4.7	0.28
2	6	4.2	3.9-4.7	0.29	8	3.9	3.5-4.5	0.23
3	17	3.8	3.3-4.3	0.15	10	3.9	3.5-4.2	0.15
4	12	3.9	3.1-4.4	0.24	9	3.8	3.2-4.5	0.25
5	7	3.9	3.6-4.5	0.23	5	4.0	3.5-4.4	0.32
6	8	4.1	3.5-4.6	0.24	10	3.8	3.3-4.5	0.21
7	3	3.7	3.5-3.9	0.24	7	3.7	3.4-4.1	0.19
8	5	3.6	3.2-4.2	0.33	10	4.0	3.3-4.9	0.31
9	11	4.1	3.5-4.8	0.25	16	4.0	3.4-4.5	0.16
10	6	4.1	4.0-4.4	0.13	6	3.8	3.1-4.5	0.37
11	8	4.0	3.7-4.3	0.16	10	4.0	3.3-4.5	0.23
12	13	4.0	3.5-4.7	0.17	15	4.1	3.2-4.7	0.21
13	18	4.4	3.7-5.2	0.16	13	4.1	3.5-4.5	0.18
14	7	4.1	3.7-4.7	0.25	8	4.1	3.8-4.5	0.16
15	11	4.0	3.5-4.5	0.19	19	3.9	3.2-4.5	0.15
16	6	4.4	3.8-4.8	0.34	5	4.2	3.8-4.5	0.27
17	19	4.0	3.6-4.4	0.13	22	3.8	3.4-4.7	0.14
18					9	4.1	3.5-4.6	0.20
19	5	4.1	3.1-4.5	0.51	17	3.9	3.2-4.6	0.18
20	11	4.1	3.6-4.9	0.30	13	4.2	3.6-4.9	0.18
21	6	4.1	3.7-4.4	0.22	7	4.0	3.5-4.6	0.31

approximates the value for the larger mice (sample 14) to the east than for smaller mice to the south (sample 17). The mean total length of males from Isla de Ometepe (sample 19) is large but only three specimens are involved and the range is so great that no definite conclusion can be drawn. Females from Isla de Ometepe have a mean total length intermediate between those that are shorter from Managua and Meseta de los Pueblos (sample 17) and those that are larger from southwestern Nicaragua and the Guanacaste region of Costa Rica. Specimens from samples 20 and 21, excepting small females from sample 21, have mean values that are large and are similar to specimens from north-central Nicaragua and Honduras.

Specimens from coastal Oaxaca, Chiapas, and Guatemala (1-5), except for males from sample 5, possess the shortest mean length of tail for the species, as they did for total length (Table 21). Of the remaining samples, only specimens from 10 (vicinity San Salvador, El Salvador), 15, 17 (both in western Nicaragua), and females from 19 (Isla de Ometepe, Nicaragua) have means of less than 115.0. The individuals with the longest mean length of tail are from the vicinity of Guatemala City (6) and adjacent parts of the valleys of Río Negro and Río Motagua (7), northwestern El Salvador (11), and Honduras (13). Specimens from Nicaragua and Costa Rica (14, 16, 18, 20, 21) tend to have somewhat shorter tails than northern populations—mean values usually being less than 120.

There appears to be no geographic pattern to the variation in length of hind foot of specimens of *Liomys salvini* (Table 21). As a matter of fact, the ranges for the various samples are almost completely overlapping. For males, mean values range from 26.4 for specimens from Honduras (13) to 29.0 for specimens from the vicinity of Guatemala City (6). For females, the range of values is from 25.4 for specimens from near Los Maderas, Nicaragua (18), to 28.8 for specimens from the vicinity of Sacapulas and Salamá, Guatemala (7). The only possibly meaningful pattern in this measurement is that specimens from western Nicaragua (15, 17) are somewhat smaller than are surrounding populations.

Cranial Measurements

Cranial measurements are discussed below in the order they were for *L. irroratus* and *L. pictus*. Males from southeastern Oaxaca and northwestern Chiapas (sample 1) have a mean greatest length of skull that is considerably shorter than the contiguous sample to the south (sample 2). This is not the case for females in which the values for the two samples are the same. With a few exceptions, the remainder of the samples of males have mean greatest length of skulls that are similar (range, 32.2-33.3) and exhibit no geographic pattern to their variation (Fig. 32 and Tables 21, 22). The two samples with the largest mean values are from Honduras (13) and the vicinity of Santa Rosa and Villa Somoza, Nicaragua (16). Males from the vicinity of Mapastepec, Chiapas (3), have a mean greatest length of skull of 31.9, which is slightly smaller than in surrounding populations. Males from the vicinity of San Salvador, El Salvador (10), average smaller in greatest length of skull than do surrounding populations as was the case also for total length and length of tail. This same situation is also true for males from western Nicaragua (15, 17). Samples of females from Oaxaca southward to San Salvador (samples 1-10), excepting those from sample 7, have means of greatest length of skull that are less than 32.0. In fact, except for sample 4 with a mean of 30.4, all remaining samples have means that fall between 31.0 and 31.8. Samples of females from eastern El Salvador, Honduras, north-central Nicaragua, and the vicinity of San José, Costa Rica (11-14, 16, 21), have somewhat larger means for greatest length of skull, values falling in the range of 32.2 to 32.7. Females from western Nicaragua (15, 17) have, along with those from sample 4, the smallest skulls of the species. The value for greatest length of skull of females from sample 18 is intermediate between that of the large specimens to the east (14) and the small specimens to the south (17). Also the value for specimens from Isla de Ometepe (19) is intermediate between values of the two samples on the adjacent mainland to the west (17, 20). Specimens from extreme southern Nicaragua and Guanacaste, Costa Rica (20), have a mean greatest length of skull that is somewhat smaller than the mean for females from the vicinity of San José, Costa Rica (21), but considerably larger than in the contiguous population to the north (sample 17).

The mean length of nasals for males (Table 21) from coastal Oaxaca, Chiapas, and southwestern Guatemala (1-4) is shorter than are means for males from the remainder of Guatemala and western El Salvador (5-9). This is also true for females from these areas, but the differences are not as great as in the males. Also, females from sample 5 have relatively short nasals and more nearly resemble, therefore, specimens from coastal areas (1-4) than inland populations (6, 7). Both males and females from the vicinity of San Salvador, El Salvador (10), have noticeably shorter nasals than contiguous samples. Both sexes from eastern El Salvador, Honduras, and north-central Nicaragua (11-14, 16) have nasals that average long, the values being similar to those for specimens from Guatemala and western El Salvador (5-9). Specimens from western Nicaragua (samples 15, 17) have noticeably shorter nasal bones than surrounding populations. Females from Isla de Ometepe, Nicaragua (19), have, on the average, nasals that are intermediate in size between populations with long nasals to the northeast (14, 16) and south (20, 21) and populations with short nasals to the northwest (17), but males from the island have a mean that is long and, therefore, more nearly resemble populations to the northeast and south. The sample of males (19) from Isla de Ometepe is made up of only five individuals and they exhibit a large amount of intrapopulational variation. Females from sample 18, again, are intermediate in size between contiguous populations to the east (14) and south (17), as they were in several other measurements studied. Specimens from Costa Rica have long nasals and resemble specimens from north-central Nicaragua and Honduras (13, 14, 16) in size. The pattern of variation for mean length of rostrum (Fig. 32 and Table 21) is exactly the same as for length of nasals with the exception that females from samples 8 to 10 all have rostral lengths that are short compared with contiguous populations.

I have been unable to detect any geographic pattern in variation in length of maxillary toothrow for either males or females of *Liomys salvini* (Table 21). The range of means for both is from 4.6 to 5.1. Specimens from northwestern samples (1-4) and from western Nicaragua tend to fall toward the lower limit of this range, but intrapopulational variation is great enough to mask these differences.

Analysis of variance for female *Liomys salvini* revealed that there was no significant difference between the means of any of the samples in length of interparietal bone (Table 21). Although a significant result was obtained for males in interparietal length, the results of SS-STP revealed that only two subsets were present.

There appears to be little significant variation in zygomatic breadth among samples of *Liomys salvini* (Table 21). Males from sample 1 are smaller in this measurement than are populations to the south, but females from sample 1 have a mean zygomatic breadth that is only one-tenth of a millimeter narrower than that at sample 2. There does appear to be a slight clinal increase in zygomatic breadth for females from sample 1 to samples 5 and 6. Males from most of El

TABLE 22.—*Results of three typical SS-STP analyses (total length, greatest length of skull, and depth of braincase) of geographic variation in* Liomys salvini. *Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
			Total length		
7	250.3		7	239.8	
11	244.3		11	237.0	
6	244.0		16	236.5	
18	241.7		12	232.0	
13	240.3		8	230.4	
16	238.3		14	230.4	
12	237.1		6	229.8	
9	236.3		13	229.3	
5	234.4		20	228.9	
14	233.0		18	227.4	
19	231.7		9	226.6	
20	230.8		21	223.8	
8	228.4		10	221.8	
17	226.1		19	219.7	
15	222.1		5	218.5	
10	221.0		15	213.5	
4	215.0		1	209.2	
1	213.2		17	209.1	
3	208.5		4	204.2	
2	207.6		3	198.8	
			2	198.3	

TABLE 22.—*Continued.*

Greatest length of skull

13	33.3	13	32.7
16	33.3	12	32.5
18	32.9	16	32.5
12	32.7	21	32.4
4	32.7	14	32.3
20	32.7	11	32.2
9	32.7	7	32.1
19	32.6	8	31.8
8	32.5	20	31.8
6	32.5	10	31.7
5	32.4	18	31.5
14	32.4	9	31.4
11	32.4	6	31.3
2	32.2	5	31.2
7	32.2	19	31.2
3	31.9	3	31.0
15	31.5	2	31.0
10	31.4	1	31.0
17	31.1	15	30.8
1	30.8	4	30.4
		17	30.2

Depth of braincase

11	8.9	21	8.8
13	8.9	7	8.7
7	8.8	11	8.7
20	8.8	1	8.7
1	8.8	13	8.6
4	8.8	12	8.6
9	8.7	18	8.6
10	8.6	20	8.6
5	8.6	2	8.6
3	8.6	9	8.6
19	8.6	16	8.5
12	8.6	6	8.5
16	8.6	3	8.5
2	8.5	4	8.4
6	8.5	5	8.4
8	8.5	14	8.4
18	8.5	8	8.4
14	8.4	10	8.3
17	8.3	15	8.2
15	8.2	19	8.1
		17	8.1

Salvador (samples 9-11) and females from western El Salvador (9, 10) are somewhat narrower than contiguous populations in Guatemala and Honduras. Both males and females from north-central Nicaragua (14) and western Nicaragua (15, 17, 18) have smaller means than do populations in Honduras (13) and Costa Rica (20, 21). The remaining samples (2-8, 12, 13, 16, 19-21 for both sexes and 11 for females) are of approximately the same size, with the range of mean zygomatic breadth being 14.8 to 15.6 for males and 14.6 to 15.4 for females.

There appears to be little or no geographic pattern to the small amount of variation present in the width of the interorbital constriction in males of *Liomys salvini* (Table 21). The range of variation of means is 6.4 to 7.0 with specimens from samples 1 to 5 having the smallest means in the species. The same situation also appears to be true for females, where the range of mean values for interorbital constriction is 6.4 to 7.2. Females from samples 1 to 4, the vicinity of Managua, Nicaragua (17), and Isla de Ometepe, Nicaragua (19), have the narrowest mean values for interorbital constriction.

Mastoid breadth also exhibits only a low level of geographic variation with means for males varying from 13.5 to 14.3 and those for females varying from 13.3 to 14.2 (Table 21). Males from sample 1 have a narrower mastoid breadth than in contiguous populations as do males from sample 10, but this is not true for females from these places. Both males and females from Nicaragua and Costa Rica (14, 15, 17-21), except for sample 16, have mastoid breadths that average narrower than in specimens from eastern El Salvador and Honduras (11-13). Particularly small means were exhibited by both males and females from the vicinity of Managua, Nicaragua (17), and females from Isla de Ometepe, Nicaragua. Males from Isla de Ometepe had a mean mastoid breadth that was similar to that of specimens from Costa Rica rather than those from the vicinity of Managua, but their intrapopulation variation was much higher than that of any other population. Females from sample 18 are intermediate in size between contiguous populations to the east (14) and to the south (17).

There does not appear to be a geographic pattern to variation in interparietal width in *Liomys salvini*, although some samples do show some unusual variation (Table 21). Females from sample 5, with a mean of 9.5, have unusually broad interparietal bones. Specimens from sample 10 are again smaller than contiguous populations. Males from sample 17 have a mean that falls toward the lower end of the range of means for northern populations. Females from Isla de Ometepe, Nicaragua (19), and specimens from the vicinity of San José, Costa Rica, have the narrowest interparietal bone of the species and are noticeably different from contiguous populations in this character.

Except for females from sample 10, all samples north of Nicaragua (1-13) have a depth of braincase that is essentially the same (Fig. 32 and Tables 21, 22). Specimens from north-central Nicaragua have noticeably shallower braincases than do contiguous populations in Honduras, but females have a mean that falls within the range of means for other northern populations. Samples from western Nicaragua (15, 17) and females from Isla de Ometepe, Nicaragua (19), have the

TABLE 23.—*Geographic variation in the configuration of the interparietal bone of* Liomys salvini. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Interparietal bone			Posterior margin of interparietal bone			
Sample	N	Undivided	Divided	N	Notched	Slightly notched	Unnotched
1	12	100.0	0	25	64.0	8.0	28.0
2	8	100.0	0	19	89.5	0	10.5
3	5	100.0	0	24	75.0	0	25.0
4	20	100.0	0	24	79.2	4.2	16.6
5	13	92.3	7.7	12	66.7	8.3	25.0
6	25	88.0	12.0	39	35.9	33.3	30.8
7	16	81.3	18.7	18	5.6	22.2	72.2
8	14	71.4	28.6	14	21.4	28.6	50.0
9	39	69.2	30.8	47	36.2	34.0	29.8
10	16	81.3	18.7	17	47.1	23.5	29.4
11	16	87.5	12.5	15	13.3	0	86.7
12	33	78.8	21.2	28	10.7	0	89.3
13	36	94.4	5.6	83	12.0	22.9	65.1
14	28	92.9	7.1	27	22.2	37.0	40.8
15	41	90.2	9.8	41	29.3	31.7	39.0
16	20	95.0	5.0	20	5.0	15.0	80.0
17	81	87.7	12.3	82	14.6	24.4	61.0
18	17	88.2	11.8	15	33.3	13.3	53.4
19	43	88.4	11.6	44	9.1	22.7	68.2
20	48	87.5	12.5	49	16.3	10.2	73.5
21	15	93.3	6.7	17	35.3	41.2	23.5

shallowest braincases in the species. Males from Isla de Ometepe as well as other samples from Nicaragua (16, 18) and Costa Rica (20, 21) are indistinguishable on the basis of the depth of braincase from samples from Honduras northward.

Qualitative Cranial Characters

Condition of interparietal bone (Table 23).—The longitudinal division of the interparietal bone appears to occur in some individuals in all samples from Central American countries except for those from extreme southwestern Guatemala. The condition reaches its highest incidence in specimens from the valley of the Río Motagua in Guatemala (8) and from southeastern Guatemala and western El Salvador (9). No individuals with divided interparietal bones were found in the 45 specimens that were examined from coastal Oaxaca, Chiapas, and southwestern Guatemala.

Samples from coastal Oaxaca, Chiapas, and Guatemala (1-5) are characterized by a high percentage, more than 60 per cent, of individuals that have an interparietal bone with a strongly notched posterior margin. The remainder of the samples from Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica

TABLE 24.—*Geographic variation in bones of the posterior portion of the nasal-premaxillary complex of* Liomys salvini. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Shape of posterior margin of nasals				Length of premaxillary bones		
Sample	N	Emarginate	Rounded	Truncate	N	Longer than nasals	Equal to nasals
1	25	44.0	12.0	44.0	26	76.9	23.1
2	21	76.2	23.8	0	24	70.8	29.2
3	24	66.7	12.5	20.8	25	92.0	8.0
4	25	64.0	8.0	28.0	25	100.0	0
5	14	78.6	7.1	14.3	14	100.0	0
6	40	87.5	0	12.5	40	97.5	2.5
7	21	90.4	4.8	4.8	21	100.0	0
8	20	60.0	15.0	25.0	20	100.0	0
9	49	85.7	4.1	10.2	49	100.0	0
10	17	70.6	5.9	23.5	17	100.0	0
11	15	33.3	6.7	60.0	15	100.0	0
12	30	43.3	6.7	50.0	29	93.1	6.9
13	88	68.2	12.5	19.3	88	100.0	0
14	28	57.1	28.6	14.3	28	100.0	0
15	43	55.8	18.6	25.6	43	100.0	0
16	20	60.0	30.0	10.0	20	100.0	0
17	82	54.9	19.5	25.6	83	100.0	0
18	18	83.3	16.7	0	17	100.0	0
19	46	39.1	23.9	37.0	46	100.0	0
20	48	66.7	10.4	22.9	48	100.0	0
21	21	9.5	9.5	81.0	19	100.0	0

have a lower percentage of individuals with this condition. In all of these samples, less than 50 per cent of the individuals have an interparietal bone with a notched posterior margin and, in fact, except for the sample from the vicinity of San Salvador, El Salvador, less than 40 per cent of the individuals have a notched interparietal.

Condition of posterior nasal region (Table 24).—Most populations of *Liomys salvini* have nasal bones with an emarginate termination, although in a few scattered populations this is not the case. The sample from the highlands of Costa Rica (21) has the lowest percentage of individuals with emarginate nasals (9.5 per cent), and samples 11 and 19 (33.3 and 39.1 per cent, respectively) also have a relatively low number of individuals with this character. The percentage of individuals with termination of the nasals rounded is relatively high in samples from Nicaragua and Costa Rica (14-21) as compared with samples to the north.

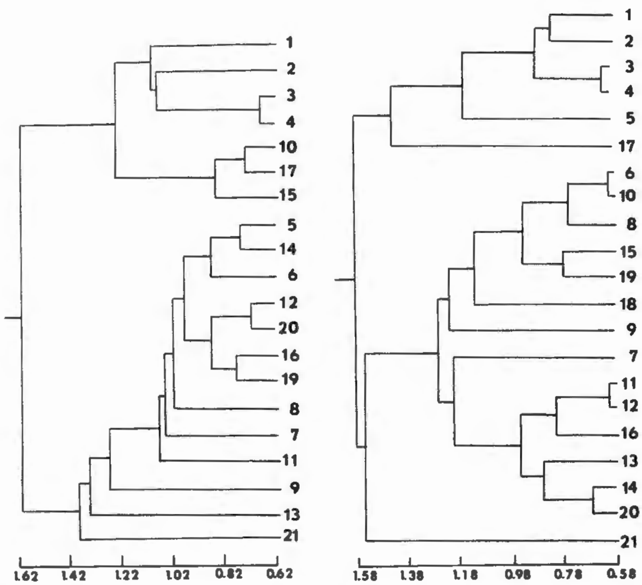


FIG. 33.—Phenograms of numbered samples (see Fig. 31 and text) of *Liomys salvini* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram for males is 0.774 and for females is 0.684.

Of the 75 specimens examined from samples 1 to 3, 15 had the nasal and premaxillary bones of the same length, whereas only two individuals in the 622 specimens examined from the remaining samples had bones of the same length. These two specimens are from the vicinity of Guatemala City (6) and southwestern coast of El Salvador (12).

Multivariate Analysis

Means of the 13 external and cranial measurements and four qualitative cranial characters were used in the NT-SYS multivariate analysis program. Phenograms diagraming the phenetic relationships of both male and female *Liomys salvini* were computed from both distance and correlation matrices; only the phenograms based upon the distance matrix (Fig. 33) are presented herein because they had larger coefficients of cophenetic correlation. In addition, a map (Fig. 34) illustrates the appropriate distance coefficient between connected samples for both sexes; in most cases distance coefficients have been given only for contiguous samples. The first three principal components were computed from the matrix of correlation among the 17 characters; these first three components combine to express 65.45 per cent of phenetic variation in males and 69.77 per cent in females.

The distance phenogram for males (Fig. 33) shows the 20 samples falling into two major clusters. The first major cluster, which includes samples 1 to 4, 10,

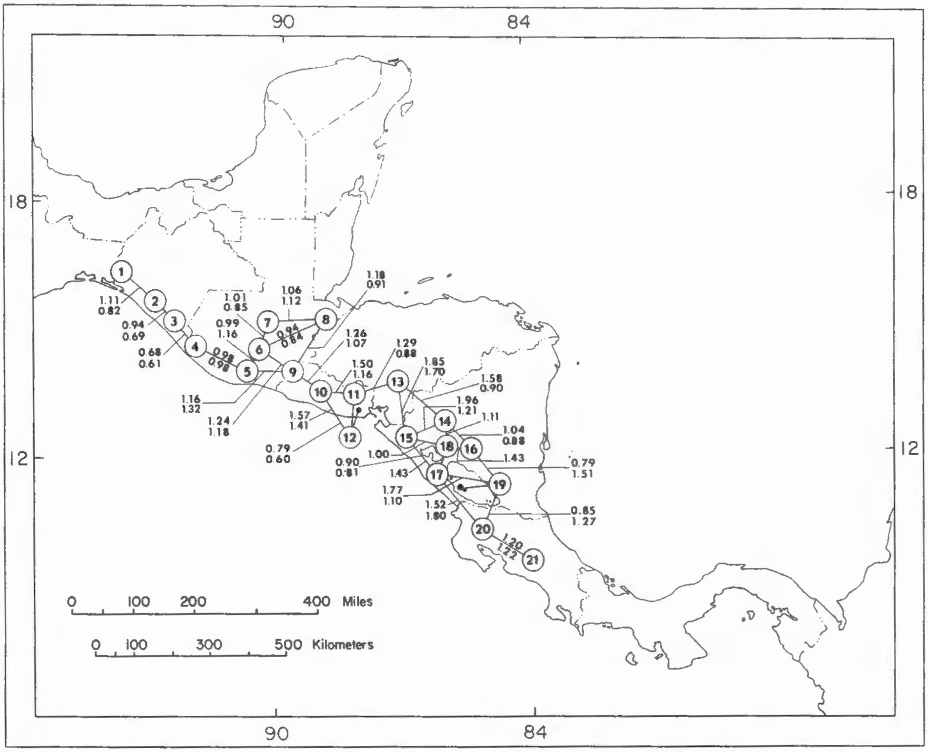


FIG. 34.—Map showing selected distance coefficients (from distance matrices) between samples of *Liomys salvini* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 31 and text for key to samples.

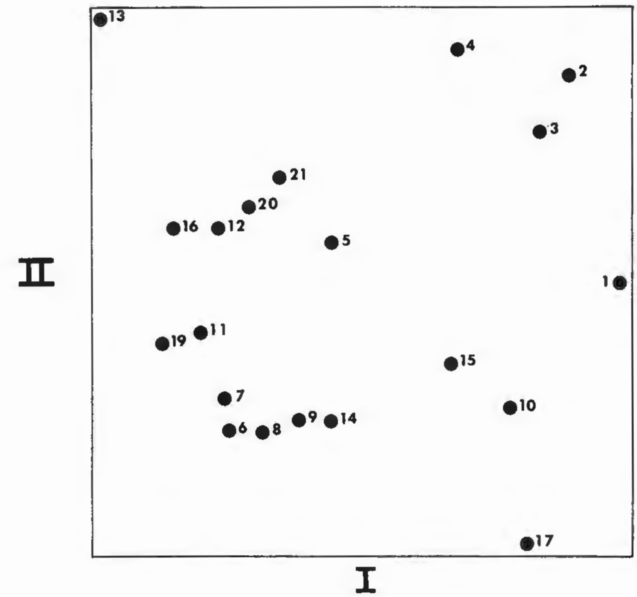
15, and 17, can be subdivided easily into subclusters of samples 1 to 4, 10, 15, and 17, with the latter division following more closely the geographical distribution of the samples. Samples 1-4 are those from coastal Oaxaca, Chiapas, and southwestern Guatemala where mice are relatively small and characterized by undivided interparietal bone, high percentage of individuals with notched interparietals, and some individuals having the nasal and premaxillary bones of equal length. Sample 10 contains individuals from the vicinity of San Salvador, El Salvador, and samples 15 and 17 contain specimens from western Nicaragua. The placing of sample 10 with 15 and 17, therefore, would be untenable on a geographic basis. The remaining samples (5-9, 11-14, 16, 19-21) form a major cluster of samples that does not appear to be easily broken into subdivisions and the samples do not appear to fall into any logical geographic sequence. Samples 13 (Honduras) and 21 (vicinity of San José, Costa Rica) appear to be relatively well differentiated from the other samples in this group, but samples 9 (southeastern Guatemala and western El Salvador) and 11 (northeastern El Salvador) fall closer to them than to other members of the group. However, separating these four samples from the others in this group on a taxonomic basis would not be tenable geographically.

The pattern of the distance phenogram (Fig. 33) for females of *Liomys salvini* is slightly different from the phenogram for males. Two basic clusters are present, but the composition of these groups has been somewhat altered. The first cluster of samples consists of 1 to 5 and 17. Sample 17 is the most "distantly" related to the other members of this group as its geographic position (vicinity of Managua, Nicaragua, as compared with coastal Oaxaca, Chiapas, and Guatemala for other samples) would indicate. Specimens from sample 5 (southern coast of Guatemala) are the next farthest removed from members of this cluster; this is probably the result of the specimens being phenetically intermediate between those from samples 1 to 4 (coastal Oaxaca, Chiapas, and southwestern Guatemala) and members of the second major cluster (remainder of Guatemala, El Salvador, and southward as is suggested by their geographic position). Sample 5 was included with the second cluster in the phenogram for males. The second major cluster of samples for females is easily subdivided into two smaller groups. The first of these subdivisions contains samples from northern and eastern Guatemala (6-8) and western El Salvador (9, 10) along with one sample from western Nicaragua (15), which was included with the first group in males, and two other samples (18, 19) from Nicaragua that had more or less intermediate values for several measurements between small individuals from sample 17 and larger individuals from samples 14 (18) and 20 (19). The second subdivision of this cluster is made up of samples from eastern El Salvador (11, 12), Honduras (13), north-central Nicaragua (14, 16), and extreme southwestern Nicaragua and Costa Rica (20, 21). All of these samples were also included in this second cluster when males were considered. Specimens from sample 21 are again quite "distant" from other members of this group.

In the principal components analysis, the amount of phenetic variation represented in the first three components for male and female *Liomys salvini*, respectively, was 42.82 and 45.13 per cent for component I, 12.70 and 13.49 for component II, and 9.92 and 11.14 for component III. Table 25 shows the weighting of each character on the first three components. The first component appears to be heavily influenced by general size as was the case for *L. irroratus* and *L. pictus*. The second component for males shows high negative values for the external measurements, interorbital constriction, and the two qualitative cranial characters dealing with the interparietal bone, whereas most of the remaining characters have relatively high positive values. The same pattern is true of the second component for females except that interorbital constriction has a low positive value. The third component for males has highest values for the qualitative cranial characters, interparietal width, and interorbital constriction; females have high values for division of the interparietal, posterior margin of the nasals, interparietal width, mastoid breadth, and interorbital constriction. Examination of two-dimensional plots (I plotted against II and I plotted against III—see Figs. 35, 36) and the three-dimensional projections (Figs. 37, 38) reveals a pattern of variation that is similar to those shown by the distance phenogram. For males, two groups of samples are formed that correspond to those of the distance phenogram. Group one can be subdivided with samples 1 to 4 being projected much

TABLE 25.—*Factor matrix from correlation among 17 characters of* Liomys salvini *studied.*

Character	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Total length	−0.888	−0.335	0.046	−0.874	−0.373	−0.222
Length of tail	−0.811	−0.383	0.037	−0.804	−0.470	−0.073
Length of hind foot	−0.465	−0.456	0.164	−0.455	−0.230	−0.530
Greatest length of skull	−0.817	0.392	0.142	−0.963	0.123	0.017
Zygomatic breadth	−0.685	0.554	0.067	−0.746	0.381	−0.021
Interorbital constriction	−0.669	−0.363	−0.447	−0.773	0.006	0.426
Mastoid breadth	−0.650	0.314	0.216	−0.717	0.441	−0.402
Length of nasals	−0.903	0.101	−0.127	−0.897	0.067	0.273
Length of rostrum	−0.922	0.113	0.009	−0.925	−0.053	0.000
Length of maxillary toothrow	−0.760	0.439	0.003	−0.675	0.443	−0.074
Depth of braincase	−0.278	0.496	−0.124	−0.517	0.548	−0.102
Interparietal width	−0.536	−0.061	0.650	0.158	0.281	−0.757
Interparietal length	−0.260	0.274	−0.117	−0.555	0.307	0.174
Posterior margin of interparietal	−0.717	−0.313	−0.182	−0.645	−0.519	0.002
Division of interparietal	−0.281	−0.445	0.229	−0.308	−0.316	−0.380
Posterior margin of nasals	−0.151	0.133	−0.883	−0.295	0.175	0.608
Length of premaxillary bones	0.564	0.383	0.229	0.382	0.669	−0.081



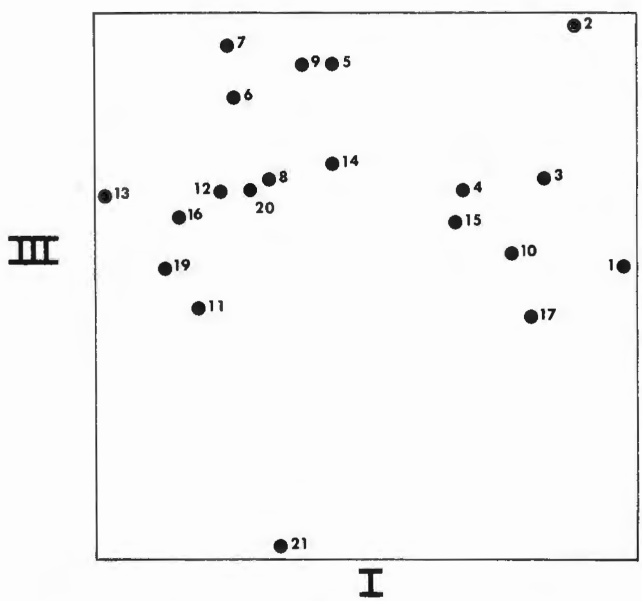


FIG. 35.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 20 samples of male *Liomys salvini*. Top, component I plotted against component II; bottom, component I plotted against component III. See Fig. 31 and text for key to samples.

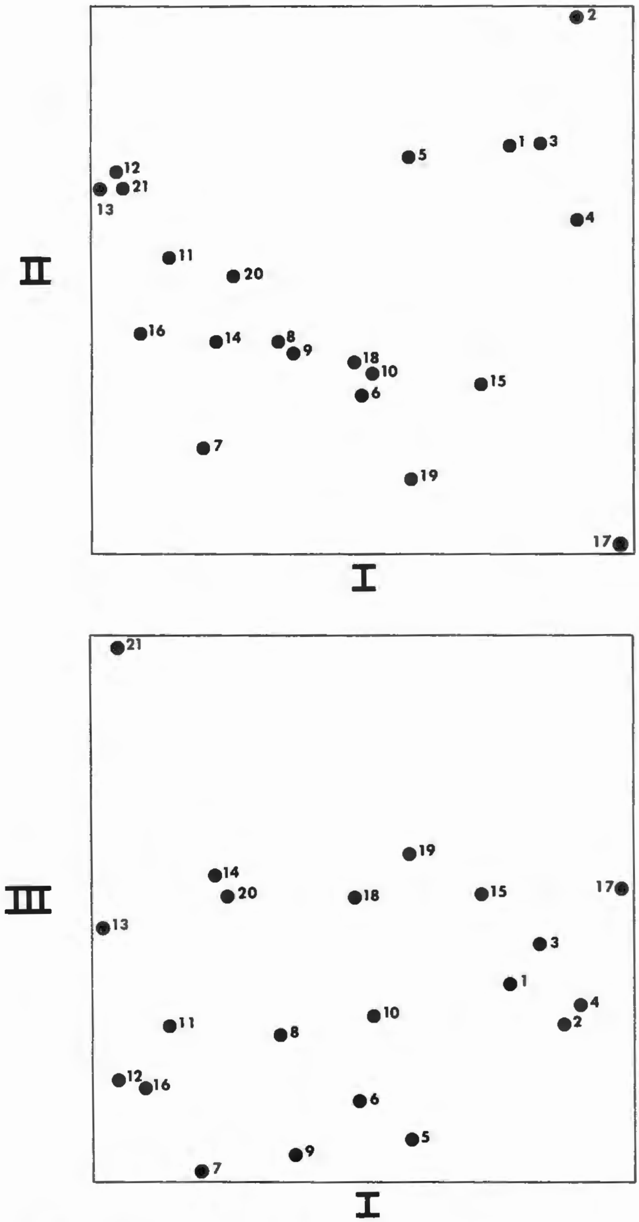


FIG. 36.—Two-dimensional projections of the first three principal components illustrating the phenetic position of the 21 samples of female *Liomys salvini*. Top, component I plotted against component II; bottom, component I plotted against component III. See Fig. 31 and text for key to samples.

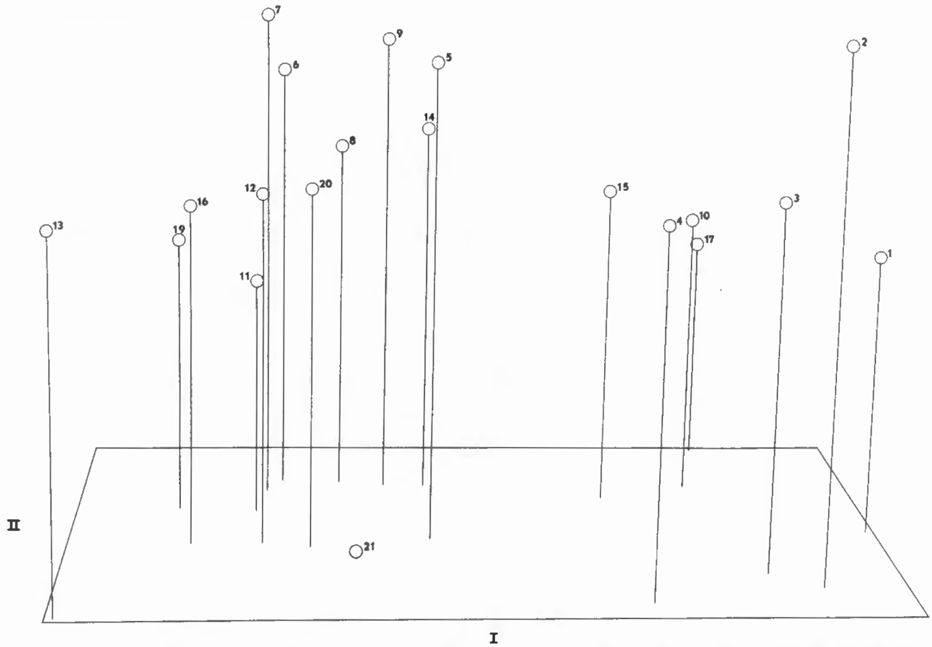


FIG. 37.—Three-dimensional projection of 20 samples of male *Liomys salvini* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 31 and text for key to samples.

closer to the front than samples 10, 15, and 17. Of note is the fact that sample 5, which occupies an intermediate geographic position between 4 and 6, falls at the lower end of the second group of samples and at a place approximately half way between samples 4 and 6. Sample 21, which was relatively "distant" from other members of the second group in the phenogram, appears to be separated from other members of the group in component III, but it should be remembered that this component represents only 9.92 per cent of the phenetic variation. Sample 13 is farthest removed from the group in component I, which represents most of the variation shown in this figure. The projection for females shows samples 1 to 4 forming one group with sample 5 again at a point almost halfway between samples 4 and 6. The placement of sample 15 with 17, as with males, does not appear to be out of the question based on this plot, although these two samples were separated in the phenogram. Sample 18 occupies a place approximately intermediate between samples 17 and 14 as does sample 19 between 17 and 20. The three-dimensional projection does not reveal as well as does the distance phenogram a definite division of the second group into two subgroups, but the samples are quite widely scattered on the first principal component where most of the variation is represented; samples 6 to 10, 18, and 19 fall at the middle of the plot and other samples of the second subdivision in the phenogram fall on the left-hand side of the plot. Sample 21 is again most "distant" from other members of

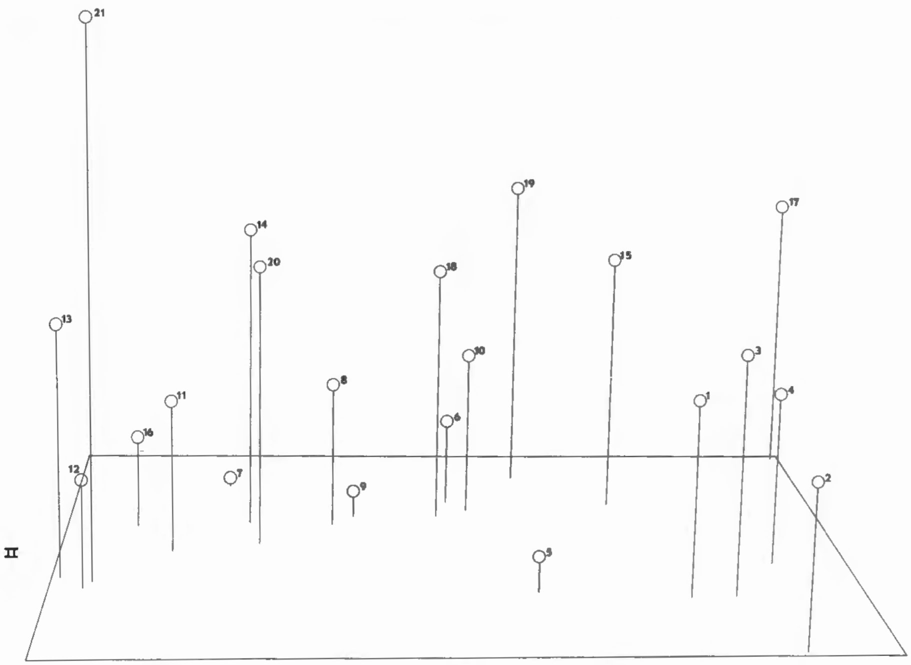


FIG. 38.—Three-dimensional projection of 21 samples of female *Liomys salvini* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Fig. 31 and text for key to samples.

the second group in the third component, but only 11.14 per cent of the phenetic variation is represented in this component.

Variation in Color

In *Liomys salvini*, as other species of the genus, variation in color appears to be more closely correlated with habitat than with systematic relationships (see Table 26 and Fig. 39). Specimens from highland areas and from the wet lowlands are dark colored, whereas specimens from dry lowlands are pale. The palest population is from Sacapulas, Guatemala, in the dry valley of the Río Negro (see Goodwin, 1934:39, pl. V, fig. 1). This population was described as *Liomys anthonyi* by Goodwin (1932*a*:2), who remarked about the extremely pale coloration of these mice. Other species of mammals from this area also tend to be pale in coloration (Packard, 1958:400; Goodwin, 1932*b*:3). Other pale populations are from along the arid valley of the Río Motagua (see Land, 1962:1-3, for a description of this area), Lake Coatepeque in El Salvador, the Cosigüina Peninsula of Nicaragua, and the vicinity of Tonalá, Chiapas, and Reforma, Oaxaca. All of these areas are relatively low and arid.

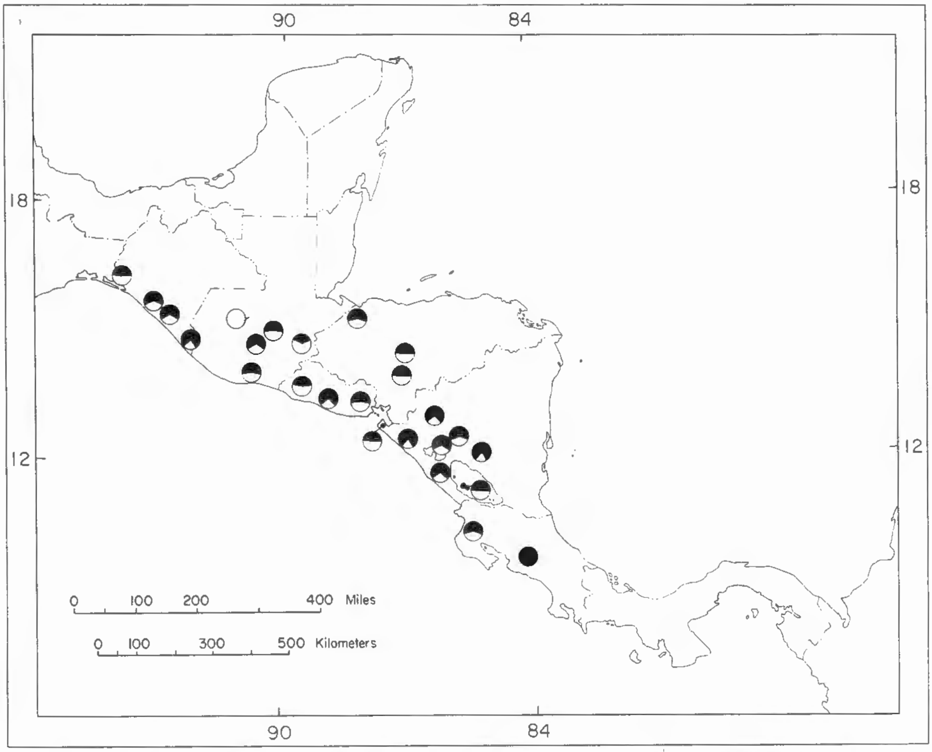


FIG. 39.—Geographic variation in red reflectance of the middorsal coloration of *Liomys salvini*. The palest sample is represented by an open symbol, the darkest sample by a completely closed symbol, and the remaining samples by symbols that are expressed as a percentage of the difference between these extremes. See Table 26 for areas represented by symbols.

The darkest individuals of *Liomys salvini* are from the highlands of Costa Rica in the vicinity of San José. Other dark populations are from Hacienda Bellavista on one of the isolated volcanos in Nicaragua, the highlands of north-central Nicaragua, highlands around Guatemala City, vicinity of San Salvador, El Salvador, two samples from the Caribbean lowlands (San Pedro Sula, Honduras, and vicinity of Santa Rosa and Villa Somoza, Nicaragua), and three samples along the Pacific coast of Chiapas and southwestern Guatemala. Again, these samples are scattered throughout the geographic range of the species and in many instances are separated from one another by populations of pale mice.

Taxonomic Conclusions

Based on the foregoing analyses, I recognize three subspecies of *Liomys salvini*. One occurs along the coast of Oaxaca, Chiapas, and southwestern Guatemala. The oldest available name for this taxon is *Liomys salvini crispus* Merriam, 1902, with type locality at Tonalá, Chiapas. The second subspecies has an ex-

TABLE 26.—*Geographic variation in dorsal coloration of 25 samples of* Liomys salvini. *Samples differ from those used for univariate and multivariate analyses. See discussion of coloration of* Liomys irroratus.

Sample	N	Red Mean ± 2 SE	Red Range	Red CV	Green Mean ± 2 SE	Green Range	Green CV	Blue Mean ± 2SE	Blue Range	Blue CV
1 (Oaxaca:Reforma; Chiapas:Tonalá)	21	12.4 ± 0.64	(10.5-17.0)	11.7	6.3 ± 0.43	(5.0-9.0)	15.7	5.8 ± 0.29	(5.0-8.0)	11.4
2 (Chiapas:Pijijiapan)	10	10.6 ± 0.78	(10.0-13.0)	11.7	5.6 ± 0.43	(5.0-7.0)	12.3	5.3 ± 0.34	(5.0-6.5)	10.1
3 (Chiapas:Mapastepec)	10	10.6 ± 0.68	(9.0-12.0)	10.1	5.5 ± 0.30	(4.5-6.0)	8.6	5.4 ± 0.28	(4.5-6.0)	10.8
4 (Chiapas:Tapachula; Guatemala:Hda. California)	14	9.6 ± 0.90	(6.5-12.0)	17.4	5.3 ± 0.40	(4.0-6.0)	14.3	5.0 ± 0.39	(3.5-6.0)	14.7
5 (Guatemala: Astillero, Iztapa)	6	11.3 ± 0.76	(9.5-12.0)	8.3	6.3 ± 0.56	(5.5-7.5)	11.0	5.9 ± 0.54	(5.0-7.0)	11.2
6 (Guatemala:Antigua, Guatemala, San Lucas)	13	10.6 ± 0.75	(8.5-13.0)	12.8	5.9 ± 0.51	(5.0-7.5)	15.6	5.5 ± 0.43	(4.5-7.0)	14.0
7 (Guatemala: Sacapulas)	10	16.5 ± 1.04	(13.0-19.0)	10.0	8.8 ± 0.75	(6.5-11.0)	13.5	7.5 ± 0.54	(6.0-9.0)	11.3
8 (Guatemala:Granados, Salama)	5	11.6 ± 1.46	(9.5-14.0)	14.1	6.2 ± 0.81	(5.0-7.5)	14.6	5.5 ± 0.63	(4.5-6.5)	12.9
9 (Guatemala:Jocotán)	10	13.6 ± 1.07	(11.5-16.5)	12.5	8.1 ± 0.69	(6.5-9.5)	13.6	7.4 ± 0.55	(6.0-8.5)	11.8
10 (Honduras:San Pedro Sula)	10	11.2 ± 0.70	(10.0-13.0)	9.9	5.8 ± 0.40	(5.0-7.0)	11.0	5.5 ± 0.43	(4.5-6.5)	12.6
11 (El Salvador:Lake Coatepeque)	10	12.5 ± 0.87	(10.5-15.0)	11.0	6.8 ± 0.62	(5.5-8.5)	14.5	6.5 ± 0.62	(5.0-8.0)	15.3
12 (El Salvador:San Salvador)	10	9.9 ± 0.30	(9.5-11.0)	4.8	5.4 ± 0.29	(5.0-6.5)	8.5	5.2 ± 0.27	(4.5-6.0)	8.1
13 (El Salvador:Divisadero, Lake Olomega, Mt. Cacaguatique)	3	11.3 ± 2.03	(9.5-13.0)	15.5	5.5 ± 0.58	(5.0-6.0)	9.1	5.3 ± 0.67	(5.0-6.0)	10.8
14 (Honduras:El Caliche Onca)	12	11.3 ± 0.62	(9.5-13.5)	9.6	5.6 ± 0.41	(5.0-7.5)	12.6	5.3 ± 0.36	(4.5-7.0)	11.7

TABLE 26.—*Continued.*

15 (Honduras:Cerro de los Cuches, La Cueva Archaga, La Flor Archaga, La Piedra de Jesus, Monte Redondo, Sabana Grande)	30	11.9 ± 0.67	(9.0-16.5)	15.5	6.0 ± 0.35	(4.5-8.0)	16.0	5.7 ± 0.31	(4.5-7.5)	15.3
16 (Nicaragua:Condega, Estelí)	8	9.4 ± 1.08	(7.5-12.5)	16.3	5.5 ± 0.57	(4.5-7.0)	14.6	4.9 ± 0.53	(4.0-6.5)	15.3
17 (Nicaragua: Esquipulas)	6	10.5 ± 1.34	(9.0-13.5)	15.6	6.0 ± 0.45	(5.5-7.0)	9.1	5.6 ± 0.48	(5.0-6.5)	10.5
18 (Nicaragua:Santa Rosa, Villa Somoza)	15	8.8 ± 0.50	(7.5-11.0)	11.1	5.2 ± 0.36	(4.0-6.5)	13.5	4.9 ± 0.30	(4.0-6.0)	11.9
19 (Nicaragua:Cosigüina)	5	12.2 ± 1.03	(11.0-14.0)	9.4	7.2 ± 0.24	(7.0-7.5)	3.8	6.8 ± 0.60	(6.0-7.5)	9.9
20 (Nicaragua:Hda. Bellavista)	10	8.8 ± 0.69	(7.0-11.0)	12.3	5.6 ± 0.48	(4.5-7.0)	13.7	5.3 ± 0.43	(4.0-6.5)	12.3
21 (Nicaragua:Las Maderas)	5	10.4 ± 1.32	(8.0-11.5)	14.2	5.9 ± 0.37	(5.5-6.5)	7.1	5.6 ± 0.37	(5.0-6.0)	7.5
22 (Nicaragua:Managua)	15	9.8 ± 0.62	(8.5-11.5)	12.2	5.3 ± 0.29	(4.5-6.5)	10.6	4.9 ± 0.24	(4.0-5.5)	9.3
23 (Nicaragua:Isla de Ometepe)	10	11.7 ± 1.09	(10.0-14.5)	14.9	6.2 ± 0.50	(5.0-7.5)	12.7	5.9 ± 0.57	(5.0-7.5)	15.4
24 (Costa Rica:Cerro de San Juan, Filadelfia, San Juanillo, Santa Rosa, Tempate)	9	10.8 ± 0.99	(8.5-13.5)	13.7	6.3 ± 0.63	(5.0-8.0)	15.0	5.9 ± 0.43	(5.0-7.0)	11.1
25 (Costa Rica:Altos Escazú, Los Higuerones, Pozos, San Francisco Esparta, San José, Santa Rosa)	11	7.2 ± 0.72	(6.0-9.5)	16.5	4.1 ± 0.43	(3.5-5.5)	17.2	4.1 ± 0.46	(3.5-5.5)	18.8

tensive geographic distribution, being found in central and eastern Guatemala, El Salvador, Honduras, north-central Nicaragua, Isla de Ometepe, Nicaragua, extreme southwestern Nicaragua, and in Costa Rica. The oldest available name for this widespread race is *Liomys salvini salvini* (Thomas, 1893), with type locality at Dueñas, Guatemala. The third subspecies of *L. salvini* is confined to the western coast of Nicaragua to the north and west of Lake Nicaragua and Lake Managua and occurs on Isla de Zapatera in Lake Nicaragua. The appropriate name for this subspecies is *Liomys salvini vulcani* (J. A. Allen, 1908), with type locality at Volcán de Chinandega, Nicaragua.

Liomys salvini crispus Merriam, 1902

1902. *Liomys crispus* Merriam, Proc. Biol. Soc. Washington, 15:49, 5 March.
1902. *Liomys crispus setosus* Merriam, Proc. Biol. Soc. Washington, 15:49, 5 March; holotype from Huehuetán, Chiapas.

Holotype.—Adult male, skin and skull, USNM 75105, from Tonalá, Chiapas; obtained on 7 August 1895 by E. W. Nelson and E. A. Goldman. Skin in good condition; skull in good condition except both zygomatic arches are broken.

Measurements of holotype.—Total length, 210; length of tail, 99; length of hind foot, 27.5; greatest length of skull, 31.8; interorbital constriction, 6.4; mastoid breadth, 13.8; length of nasals, 12.2; length of rostrum, 13.5; length of maxillary toothrow, 5.0; depth of braincase, 9.0; interparietal width, 8.6; interparietal length, 4.3.

Distribution.—Coastal areas of southeastern Oaxaca, Chiapas, and southwestern Guatemala from Reforma, Oaxaca, in the north to vicinity of Mazatenago, Guatemala, in the south (Fig. 40).

Comparisons.—From *Liomys salvini salvini* geographically adjacent to the east and south, *Liomys salvini crispus* can be distinguished by its shorter total length and length of tail (compare values of samples 1-4 with those of 6-14 in Table 21) and by a unique set of qualitative cranial characters. Samples of *crispus* have slightly smaller means than samples of *salvini* in some cranial measurements, but in most instances these are at best small average differences. The only possible exceptions are length of nasals and length of rostrum, both of which are relatively short in *crispus*. No individuals of *crispus* examined had the interparietal bone divided, but at least some individuals had the bone divided in all populations of *salvini* (see Table 23). Samples of *crispus* have a much higher percentage of individuals with the posterior margin of the interparietal bone deeply notched (more than 64 per cent) than samples of *salvini* (all except sample 5, which is intermediate in several characters that will be discussed later, have less than 50 per cent with deep notches and most have less than 40 per cent—see Table 23).

Comparison of *Liomys salvini crispus* with *Liomys salvini vulcani* is given in the account of that subspecies.

Remarks.—Merriam (1902:49) described *crispus* as a species distinct from *salvini* and Goldman (1911:46-47) maintained this arrangement in his revision of the genus. The only difference that Goldman (1911:50-51) noted between the two "species," however, was that *salvini* had a "distinctly tawny" dorsum, whereas specimens of *crispus* from Huehuetán, Chiapas, showed no trace of this color. My analysis of the variation in this group reveals that the relationships between these two taxa is best expressed by considering *crispus* as a subspecies of the earlier named *salvini. L. s. crispus* appears to intergrade with the nominal race along the southern coast of Guatemala (see discussion in the account of *L. s. salvini*).

Both Merriam and Goldman recognized specimens from Huehuetán, Chiapas, as a race of *crispus* distinct from the nominal subspecies from Tonalá, Chiapas. The specimens from Huehuetán were known under the subspecific name *setosus* and were distinguished from the typical race by their darker color and larger size. Specimens from the vicinity of Tonalá are paler than those from southern Chiapas, but color is a highly variable character and is not a good indicator of geographic variation. Males from northern Chiapas are somewhat smaller than their counterparts in the south, but females from the two areas are essentially the same size. Based on both univariate analysis and multivariate analysis, the relationship of the populations from Chiapas and adjacent areas in Guatemala and Oaxaca is best recognized by assigning them to a single taxon, *Liomys salvini crispus*.

The small size of the males from the vicinity of Tonalá, Chiapas, and Reforma, Oaxaca, is of interest because this is the area in which *Liomys salvini* is sympatric with *Liomys pictus*. In the account of *Liomys pictus pictus*, it was pointed out that males from southeastern Oaxaca and northwestern Chiapas were larger than males from adjacent populations of *pictus*. One explanation for this unusually large size of one species and small size of the other from the only area of sympatry would be that character displacement may be involved. A more detailed discussion of this situation is given in a following section on specific relationships.

An adult male from 3 mi. W Mazatenago, Guatemala (KU 65032), was not included in the univariate and multivariate analyses because the specimen was from a geographical area intermediate between sample 4 and sample 6 and an *a priori* judgment could not be made as to which sample the specimen should be allocated. However, comparison of the measurements of the specimen from Mazatenago (total length, 211; length of tail, 107; greatest length of skull, 31.4; length of nasals, 11.5; length of rostrum, 13.3) with the values for specimens from samples 4 and 6 reveals that it more closely agrees with values for specimens from sample 4, and therefore, should be assigned to the subspecies *crispus*. Also the specimen has an undivided interparietal bone and the posterior margin of the interparietal has a relatively deep notch; both of these characteristics are typical of *crispus*. An adult male (AMNH 79240) from San Lucas, approximately 40 kilometers east-northeast of Mazatenago, has large external and cranial measurements (total length, 255; length of tail, 127; length of nasals, 12.3; length of rostrum, 14.1) and other characteristics that are typical of *L. s. salvini*. Based on this evidence it would appear that the two subspecies come into contact in this area somewhere along the slopes of the Guatemalan highlands between Mazatenago and San Lucas.

Mean values for five adult males and adult (nonpregnant) females from southern Chiapas, respectively, for length of ear were 13.2 (12.0-14.0) and 13.4 (12.0-15.0), and for weight were 45.1 (37.2-55.0) and 37.0 (28.1-46.0).

Specimens examined (151).—GUATEMALA: Hacienda California, San Marcos, 13 (AMNH); 3 mi. W Mazatenago, 1280 ft., Suchitepéquez, 1 (KU).

CHIAPAS: 11 mi. NW Escuintla, 100 ft., 4 (2 LACM, 2 UA); Estación Vieja, 1 km. S Mapastepec, 46 m., 3 (UNAM); Guatimoc, 1 (ENCB); Huehuetán, 14 (USNM); 13.5 km. (Huixtla-Motozintla Road) NE Huixtla, 250 m., 1 (UMMZ); Mapastepec, 45 m., 28 (UMMZ); Pijijiapan, 10 m., 20 (UMMZ); 20 km. SE Pijijiapan, 3 (LACM); 1 mi. SE Puerto Madero, 4 (KU); Talisman, 3 (AMNH); Tapachula, 4 (AMNH); 16 km. SW Tapachula, 35 m., 11 (KU); 12 mi. S Tapachula, 5 (AMNH); 6 mi. NW Tonalá, 9 (KU); Tonalá, 19 (USNM); approximately 12½ km. SE Tonalá, 1 (LACM).

OAXACA: Reforma, 7 (UMMZ).

Marginal records.—OAXACA: Reforma. CHIAPAS: 6 mi. NW Tonalá; *Tonalá*; approx. 12½ km. SE Tonalá; Pijijiapan; 20 km. SE Pijijiapan; Mapastepec; *11 mi. NW Escuintla*; 13.5 km. (Huixtla-Motozintla Road) NE Huixtla; Guatimoc. GUATEMALA: 3 mi. W Mazatenago; Hda. California hence northward along the coast.

Liomys salvini salvini (Thomas, 1893)

1893. *Heteromys salvini* Thomas, Ann. Mag. Nat. Hist., ser. 6, 11:331, April.

1911. *Liomys salvini*, Goldman, N. Amer. Fauna, 34:50, 7 September.

1893. *Heteromys salvini nigrescens* Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:234, September; holotype from an unknown locality in Costa Rica (Goodwin, 1946:374, suggested that "the type came from an accessible part of Costa Rica, probably Escazú").

1902. *Liomys heterothrix* Merriam, Proc. Biol. Soc. Washington, 15:50, 5 March; holotype from San Pedro Sula, Cortés, Honduras.

1932. *Liomys anthonyi* Goodwin, Amer. Mus. Novit., 528:2, 23 May; holotype from Sacapulas, 4500 ft., El Quiché, Guatemala.

1938. *Liomys salvini aterrimus* Goodwin, Amer. Mus. Novit., 987:4, 13 May; holotype from Sabanillas de Pirrís, about 3730 ft., San José, Costa Rica.

Holotype.—Adult male, skin and skull, BMNH 75.2.27.35, from Dueñas, Sacatepéquez, Guatemala; obtained on 31 July 1873 by Osbert Salvin. Skin in fair condition, but no external measurements listed; skull in good condition.

Measurements of holotype.—Greatest length of skull, 32.8; zygomatic breadth, 15.0; interorbital constriction, 7.3; mastoid breadth, 14.1; length of nasals, 12.5; length of rostrum, 14.2; length of maxillary toothrow, 5.4; depth of braincase, 9.3; interparietal width, 9.9; interparietal length, 4.6.

Distribution.—Guatemala (along the southern coast, in the highlands around Guatemala City, and in the valleys of the Río Negro and Río Motagua as far as San Pedro Sula, Honduras), most of El Salvador, south-central Honduras, north-central and central Nicaragua, Isla de Ometepe in Lake Nicaragua, extreme southwestern Nicaragua, and western and central Costa Rica (Fig. 40).

Comparisons.—Comparison of *Liomys salvini salvini* with *Liomys salvini crispus* and *Liomys salvini vulcani* is given in the accounts of those subspecies.

Remarks.—*Liomys salvini salvini* has an extensive geographic range in Central America. It is characterized by large external and cranial dimensions, at least some individuals in each sample having the interparietal bone divided, and a low percentage of individuals having the posterior margin of the interparietal

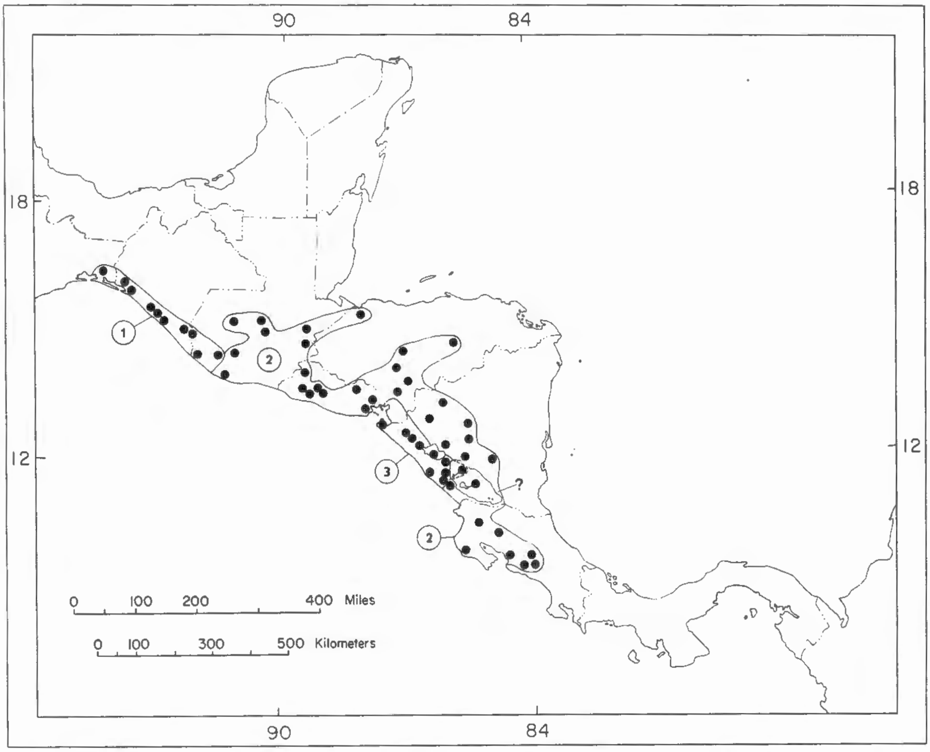


FIG. 40.—Geographic distribution of subspecies of *Liomys salvini*: 1, *L. s. crispus*; 2, *L. s. salvini*; 3, *L. s. vulcani*. The occurrence of *L. s. salvini* to the east of Lake Nicaragua is questionable at present.

deeply notched. With few exceptions, samples of *L. s. salvini* exhibited rather uniform values for external and cranial measurements (Table 21); this was not true, however, for color (Table 26).

Specimens assigned to *L. s. salvini* from southwestern Nicaragua and Costa Rica may not be in contact with other populations of the subspecies in central Nicaragua (vicinity of Boaco), because mice from the northwestern edge of Lake Nicaragua at Hacienda Mecatepe and from Isla de Zapatera appear to represent *L. s. vulcani,* thus causing a break in the distribution of *salvini* along the western side of Lake Nicaragua. Despite this apparent break in the geographic range, I have assigned specimens from the southern segment to *salvini* because of their close morphological resemblence to other members of that taxon. In both the univariate and multivariate analyses, specimens from southwestern Nicaragua and Costa Rica exhibited little or no differentiation from samples from central and north-central Nicaragua and south-central Honduras. There are several possible explanations for this situation. One of the more likely would seem to be that the two segments of the population of *L. s. salvini* recently have been in contact along the western side of Lake Nicaragua and agriculturization, recent volcanic action, or some other disturbance has resulted in immigration of *vulcani* into this area (or at least allowed the spread of *vulcani*-like characteristics). Another possibility is that the two segments are at present in contact around the eastern side of Lake Nicaragua, but the likelihood of this situation is lessened by the fact that a large collection of mammals from La Esperanza, just south of San Carlos at the southeastern edge of Lake Nicaragua, does not contain specimens of *Liomys salvini*. The possibility exists, however, that during a period when climatic conditions were different from at present, contact between the populations or colonization of Costa Rica could have occurred along the eastern side of Lake Nicaragua. Moreover, it could be that some genetic contact is maintained between the two populations across Lake Nicaragua as might be indicated by the fact that specimens from Isla de Ometepe are assignable to *salvini* (although in several measurements females from the island had values that were intermediate between those for *vulcani* and *salvini*), although this would seem to be extremely unlikely. In order for this type of contact to be effective, large numbers of mice would need to be transported across the lake because the genetic complement of a small number of invaders would be swamped by resident populations. Another possibility that should not be overlooked is that when additional material is available from the northwestern edge of Lake Nicaragua, especially from the vicinity of Grenada, these populations may be found to be properly assignable to *salvini*, not *vulcani*. Finally, an explanation that I regard as highly unlikely, but which cannot be completely disregarded, is that these two populations have long been separated and that they have come to resemble each other morphologically owing to similar selective pressures.

In summary, populations assigned to *salvini* from southwestern Nicaragua and Costa Rica, and those from central Nicaragua are probably not now in geographic contact, but probably were in contact in the recent past. The discontinuity evidently is sufficiently recent that the two segments exhibit little or no differentiation, certainly not enough to warrant taxonomic recognition. If for some reason the population in southwestern Nicaragua and Costa Rica were to be considered a distinct race, the name *Liomys salvini nigrescens* (Thomas, 1893) is available for it.

Two species (*anthonyi* Goodwin, 1932, and *heterothrix* Merriam, 1902) and two subspecies (*nigrescens* Thomas, 1893, and *aterrimus* Goodwin, 1938) formerly considered to be distinct are placed herein as junior synonyms of *salvini*. Material from the type locality of *L. anthonyi* (Sacapulas, Guatemala) is included in sample 7 and material from the type locality of *L. heterothrix* (San Pedro Sula, Honduras) is included in sample 8. When these two samples were compared with one another and with material from the type locality of *L. salvini* (sample 6), little difference was noted between them in either the univariate or multivariate analysis. Males from the three samples are particularly close in the multivariate analysis. Specimens from these samples do, however, exhibit extreme variation in color. Those from the vicinity of the type locality of *salvini* are the darkest of this group (10.6 red reading), although specimens from the vicinity of Granados and Salamá near the headwaters of the Río Motagua and just north of the type locality are also dark (11.6 red reading) as are specimens from the Caribbean lowlands at San Pedro Sula, Honduras (11.2 red reading). Specimens from Sacapulas, in the dry valley of the Río Negro, are the palest of the species with a red reading of 16.5; also, specimens from along the Río Motagua northeast of the type locality of *salvini* are pale (red reading 13.6). There appear to be two disjunct pale and two disjunct dark populations existing in this area; recognition of all four of these populations as distinct would obscure their overall resemblence in mensural data and qualitative cranial characteristics.

Liomys salvini nigrescens was named by Thomas (1893*b*:234) on the basis of a single specimen from an unknown locality in Costa Rica. The holotype of *nigrescens* was described as differing from the holotype of *salvini* by its darker color and smaller size. Material from the highlands of Costa Rica where subsequent authors have supposed the holotype was obtained (see particularly Goodwin, 1946:374) represents the darkest population of *salvini* that I have examined, but in mensural characteristics these specimens and the holotype of *nigrescens* (BMNH 69.7.19.6) fall within the range of variation of samples I have assigned to *salvini*. On the basis of the above data, I have placed *nigrescens* in the synonymy of *salvini*, although as was discussed earlier in this section, if the disjunct population from southwestern Nicaragua and Costa Rica should prove to be distinct, then *nigrescens* would be the oldest available name for this taxon.

Goodwin (1938:4-5) described *Liomys salvini aterrimus* on the basis of a single adult female from Sabanilla de Pirrís, distinguishing it on basis of dark coloration and long tail. The holotype (FMNH 35211) is extremely dark in color, but it could be matched by other specimens from San José in similar pelage. The length of tail of the specimen does fall at the upper extreme for sample 21, but it is not much longer than in other members of the sample and can be matched in other samples (such as 12 and 13). On the basis of the data presently available, even though the specimen from Sabanilla de Pirrís exhibits extreme variation in two characters, to accord it taxonomic recognition would obscure the numerous similarities in other characteristics, such as size and qualitative characters of the cranium, with mice from adjacent areas.

Specimens from the southern coast of Guatemala (sample 5) show some characteristics that are intermediate between populations of *crispus* to the northwest along the coast and *salvini* in the highlands to the north and east. In several characters (length of tail, length of nasals, length of rostrum) of the univariate analysis, females more closely resembled *crispus* than *salvini*, although males had values that were similar to *salvini* in these characters. In the multivariate analyses, the females were more or less intermediate between samples of *crispus* and *salvini*, whereas males fell toward the lower limit of the *salvini* samples. A high percentage of specimens in sample 5 have the posterior margin of the interparietal bone deeply notched (66.7 per cent), which is characteristic of *crispus*, but one of the 13 specimens for which data were recorded had the interparietal bone divided, which is characteristic of *salvini*. The southern coast of Guatemala is an area of intergradation between the races *crispus* and *salvini*, but in overall characteristics the sample is somewhat more *salvini*-like and has been assigned to that race. The specimen from the marginal locality, Tiquisate, Guatemala, is young and subspecific allocation is impossible, but specimens from the nearby locality of Concepción del Mar indicate affinities with *salvini* for specimens from the area.

Females from 8 km. N Las Maderas, Nicaragua, are intergrades between *L. s. salvini* in the highlands to the east and north and *L. s. vulcani* in the lowlands to the west and south. In many cranial measurements, females of sample 18 have values that are intermediate between those of samples 14 and 17, but in external measurements, interorbital constriction, and depth of braincase, they are more nearly like females of *salvini* from sample 14. In the multivariate analysis, sample 18 is near the lower limit of the range of variation for *salvini*, but it still falls within it and for that reason I have assigned the specimens to *salvini*. Two adult males from 11 mi. SE Dario, which is about 12 kilometers north of the Las Maderas locality, appear to represent typical *L. s. salvini* with no indication of intergradation with *vulcani*. Contact between populations of *salvini* and *vulcani* south of the Meseta de las Pueblos is discussed in the account of the latter subspecies.

The sample from the vicinity of San Salvador, El Salvador (sample 10), is the one exception to the relatively uniform size of specimens of *Liomys salvini salvini*. In the univariate analysis both males and females (especially males) from the vicinity of San Salvador were uniformly smaller than specimens of the corresponding sex from surrounding areas. The females do fall at the lower edge of the range of variation for samples of *salvini* in the multivariate analysis, but the males fall well below the limit of other *salvini* samples. Whether this is a result of a sampling error or a differentiated population in the vicinity of San Salvador will not be known until more material from this area is available. For the present, I believe it is best to assign these specimens to *salvini*.

Specimens from Monte Rey, 22 kn. S San José, Costa Rica, represent the southernmost known record for the species. This locality is approximately 300 kilometers northwest of the nearest known locality of *Liomys adspersus*, the intervening area evidently uninhabited by *Liomys*.

The average length of ear of 10 adult males and 10 adult females of *Liomys salvini salvini* from northern and central Nicaragua was, respectively, 14.4 (13.0-16.0) and 14.0 (12.0-16.0); these same animals had mean weights of 54.9 (42.1-65.2) and 43.5 (38.2-50.8).

Specimens examined (914).—COSTA RICA: Altos Escazú, San José, 3 (1 AMNH, 2 MCZ); ½ km. S Bagaces, Guanacaste, 1 (TCWC); Boca del Barranca, Puntarenas, 1 (LACM); 1 mi. E Cangrejal, San José, 3 (LSU); Cerro de San Juan, 1200 ft., Guanacaste, 4 (UMMZ); Esparta, 300 ft., Puntarenas, 1 (FMNH); 7 mi. SW Filadelfia, Guanacaste, 4 (KU); Finca Coyolar, 5 km. N, 2½ km. W Liberia, Guanacaste, 5 (LACM); Finca Jiménez, Guanacaste, 2 (MVZ); ½ mi. E Finca Jiménez Headquarters, 30 m., Guanacaste, 7 (UMMZ); 1 8/10 mi. by road NE Las Cañas, Guanacaste, 1 (LSU); 5 mi. N Liberia, Guanacaste, 1 (LACM); 4 4/10 mi. N Liberia, Guanacaste, 1 (LACM); 9 km. N Liberia, 4 km. E Interamerican Highway, Guanacaste, 2 (LACM); 4½ mi. S Liberia, Guanacaste, 5 (LACM); Los Higuerones, San José, 3 (AMNH); Monte Rey, 22 km. S San José, 1100 m., San José, 4 (KU); Playa del Cocos, Guanacaste, 4 (LACM); 3 km. S Playa del Cocos, Guanacaste, 12 (LACM); 1½ mi. SE Playa del Cocos, Guanacaste, 5 (LACM); Pozos, *ca.* 1 km. N Santa Ana, San José, 1 (LSU); Río Bebedero, 2 km. S Bebedero, 5 m., Guanacaste, 1 (KU); Río Grande, Villa Colon, San José, 13 (10 FMNH, 3 USNM); Río Tenorio, 3 mi. S, 10 mi. W

Las Cañas, 10 ft., Guanacaste, 1 (TCWC); Río Teopisco, Pan American Highway 30 mi. S Nicaraguan border, 250 ft., Guanacaste, 2 (KU); Sabanilla de Pirrís, San José, 1 (FMNH); San Francisco Esparta, Puntarenas, 1 (AMNH); San Juanillo, 100 ft., Guanacaste, 1 (UMMZ); 6 mi. SSE San Ignacio, San José, 1 (LSU); 1 mi. N Santa Ana, San José, 1 (LSU); *ca.* 2 km. NW Santa Ana, San José, 5 (LSU); 3 mi. N Santa Rosa, Guanacaste, 2 (KU); Tempate, 150 ft., Guanacaste, 3 (2 MCZ, 1 UMMZ); 1 7/10 mi. by road W Tilarán, Guanacaste, 1 (LSU); unknown locality, 1 (BMNH).

El Salvador: Barra de Santiago, sea level, Ahuachapan, 2 (MVZ); Divisadero, Morazán, 1 (UMMZ); ¾ mi. NE Divisadero, 1000 ft., Morazán, 5 (MVZ); 1 mi. SE Divisadero, 850 ft., Morazán, 11 (MVZ); El Tablón, Lake Guija, 1450 ft., Santa Ana, 3 (MVZ); Hacienda Chilata, 2000 ft., Sonsonate, 10 (MVZ); Lake Coatepeque, Santa Ana, 43 (AMNH); SW edge Lake Olomega, 200 ft., San Miguel, 29 (28 MVZ, 1 UMMZ); 1 mi. S Los Planes, San Salvador, 2 (KU); Monte Cristo Mine, 700 ft., Morazán, 5 (MVZ); Mt. Cacaguatique, 3500 ft., San Miguel, 9 (8 MVZ, 1 UMMZ); Pine Peaks, 3 mi. W Volcán Conchagua, 3400 ft., La Union, 4 (3 MVZ, 1 UMMZ); Puerto del Triunfo, sea level, Usulután, 8 (7 MVZ, 1 UMMZ); Río Goascorán, 13° 30′ N, 100 ft., La Union, 1 (MVZ); Río San Miguel, 13° 25′ N, 225 ft., San Miguel, 4 (MVZ); 2 mi. SE San Cristóbal (Guatemala), 2950 ft., Santa Ana, 1 (KU); 1 mi. NW San Salvador, San Salvador, 13 (KU); 6 mi. E San Salvador, San Salvador, 3 (KU); 10 mi. NW Santa Tecla, La Libertad, 3 (KU); Volcán de San Miguel, 1900 ft., San Miguel, 17 (16 MVZ, 1 UMMZ).

Guatemala: Antigua, Sacatepéquez, 2 (AMNH); Astillero, 25 ft., Escuintla, 7 (KU); Cabañas, Zacapa, 5 (USNM); 5 mi. S Chiquimulilla, 200 ft., Santa Rosa, 1 (KU); Concepción del Mar, Escuintla, 2 (FMNH); 2 mi. N, 1 mi. W Cuilapa, 2980 ft., Santa Rosa, 1 (KU); Dueñas, Sacatepéquez, 1 (BMNH); El Rancho, El Progreso, 7 (FMNH); 4 mi. W Escuintla, 880 ft., Escuintla, 2 (KU); Finca Cruz, 6 8/10 mi. SW Progreso, 1870 ft., El Progreso, 3 (USNM); Finca El Carnero, Cerro las Flores, 2100 ft., Jutiapa, 1 (UMMZ); Finca Los Arcos, Escuintla, 3 (USNM); Finca Valle-Lirios, Escuintla, 5 (USNM); Gualán, Zacapa, 14 (ANSP); 4 mi. S Guatemala City, 4700 ft., Guatemala, 1 (KU); 5 mi. S Guatemala City, 4950 ft., Guatemala, 4 (KU); 2 3/10 mi. W, ¼ mi. N Iztapa, Escuintla, 6 (KU); Jocotán, 1350 ft., 3 (KU); 3 mi. E Jocotán, 1400 ft., Chiquimula, 24 (KU); Km. 24 on highway S Guatemala City, Guatemala, 48 (18 AMNH, 30 KU); Km. 27 on highway S Guatemala City, 4100 ft., Guatemala, 1 (KU); Km. 33 on highway S Guatemala City, 4000 ft., Escuintla, 1 (KU); Km. 52 on highway S Guatemala City, 1650 ft., Escuintla, 1 (KU); S side Lake Amatitlán, 4200 ft., Guatemala, 12 (USNM); Lake Atescatempa, 2400 ft., Jutiapa, 20 (USNM); La Primavera, Alta Verapaz, 2 (AMNH); 1 mi. SE Monogoy, Jutiapa, 10 (KU); Progreso, El Progreso, 1 (AMNH); Puente Punta Gordo, 2050 ft., El Progreso, 1 (KU); 1 mi. S Rabinal, 3450 ft., Baja Verapaz, 2 (KU); Río Grande, 3 mi. S, 1½ mi. W Granados, 2000 ft., Baja Verapaz, 7 (KU); Río Guacalate, 1 mi. W Masagua, Escuintla, 5 (USNM); Río Santiago, 152 km. NE Guatemala City, 500 ft., Zacapa, 5 (KU); Río Wite, 5 2/10 mi. E Cabañas, Zacapa, 5 (USNM); Sacapulas, El Quiché, 21 (AMNH); ½ mi. N, 1 mi. E Salamá, 3200 ft., Baja Verapaz, 2 (KU); 2½ mi. W, 2¼ mi. N San Cristóbal, 2900 ft., Jutiapa, 4 (KU); San José, 15 ft., Escuintla, 9 (USNM); San Lucas, Sololá, 3 (AMNH); Tiquisate, Escuintla, 1 (FMNH); Trujillo, Zacapa, 3 (USNM); Volcán San Lucas, Sololá, 1 (AMNH).

Honduras: Catacamas, Olanche, 1 (AMNH); Cerro de los Cuches, Sabana Grande, Francisco Morazán 8 (AMNH); 1 mi. S Comayagüela, 1000 m., Francisco Morazán, 1 (TCWC); El Caliche Orica, Francisco Morazán, 12 (AMNH); Escuela Agricultura Panamericana, Francisco Morazán, 14 (MCZ); Hatillo, Francisco Morazán, 2 (MCZ); La Cueva Archaga, Francisco Morazán, 6 (AMNH); La Flor Archaga, Francisco Morazán, 10 (MCZ); La Piedra de Jesús, Sabana Grande, Francisco Morazán, 66 (AMNH); 2 mi. S La Venta, 420 m., Francisco Morazán, 2 (TCWC); Monte Redondo, Francisco Morazán, 47 (12 AMNH, 8 FMNH, 20 MCZ, 4 UMMZ, 3 USNM); Sabana Grande, Francisco Morazán, 1 (AMNH); San Pedro Sula, Cortés, 20 (USNM); 12 mi. N Tegucigalpa, 2800 ft., Francisco Morazán, 1 (TCWC); Toncontín, Francisco Morazán, 1 (MCZ).

NICARAGUA: 1½ km. W Alta Gracia, 110 m., Isla de Ometepe, Rivas, 6 (KU); 4 km. S, 1½ km. E Alta Gracia, 40 m., Isla de Ometepe, Rivas, 13 (KU); Finca Amayo, 13 km. S, 14 km. E Rivas, 40 m., Rivas, 7 (KU); 14 km. S Boaco, 220 m., Boaco, 2 (KU); 8 mi. S Condega, Estelí, 6 (KU); Darailí, 5 km. N, 14 km. E Condega, 940 m., Estelí, 5 (KU); 11 mi. SE Dario, Matagalpa, 7 (KU); 1 km. NE Esquipulas, 420 m., Matagalpa, 20 (KU); 9 mi. NNE Estelí, Estelí, 7 (KU); Hacienda Tepeyac, Matagalpa, 2 (1 KU, 1 USNM); 1 mi. NW Jinotega, Jinotega, 1 (KU); La Danta, 1 km. N, 5 km. E Esquipulas, 780 m., Matagalpa, 2 (KU); 8 km. (by road) N Las Maderas, 380 m., Managua, 20 (KU); Matagalpa, Matagalpa, 1 (AMNH); 2 km. N Mérida, 40 m., Isla de Ometepe, Rivas, 2 (KU); 2 km. N, 3 km. E Mérida, 200 m., Isla de Ometepe, Rivas, 7 (KU); Moyogalpa, NW end Isla de Ometepe, 40 m., Rivas, 14 (KU); 5 km. E Moyogalpa, Isla de Ometepe, Rivas, 3 (KU); 6 km. E Moyogalpa, Isla de Ometepe, Rivas, 19 (KU); Quilalí, Nueva Segovia, 2 (AMNH); Río Javillo, 3 km. N, 4 km. W Sapoá, 40 m., Rivas, 3 (KU); 11 km. S, 3 km. E Rivas, 50 m., Rivas, 1 (KU); 3 mi. SE San Pablo, Rivas, 1 (KU); 3 mi. E San Ramon, Matagalpa, 1 (KU); Santa Rosa, 17 km. N, 15 km. E Boaco, 300 m., Boaco, 17 (KU); 1 km. NW Sapoá, 40 m., Rivas, 1 (KU); Savala, Matagalpa, 1 (AMNH); Sébaco, Matagalpa, 2 (AMNH); Uluce, Matagalpa, 6 (AMNH); 1 km. N, 2½ km. W Villa Somoza, 330 m., Chontales, 8 (KU).

Additional records.—COSTA RICA: Cañas, Guanacaste (Esquivel *et al.*, 1967:954); Cangrejal, San José (Esquivel *et al.*, 1967:954); Finca Coyolar, 5 km. N, 4 km. W Liberia, Guanacaste (Webb and Loomis, 1971:5); 8.3 km. N Liberia, Guanacaste (Webb and Loomis, 1971:36); 2 km. W Liberia, Guanacaste (Geest and Loomis, 1968:38); 7.3 km. S Liberia, Guanacaste (Geest and Loomis, 1968:38); 7.5 km. S Liberia, Guanacaste (Webb and Loomis, 1971:36); 5 km. NW Tilarán (Geest and Loomis, 1968:25); Santa Ana, San José (Esquival *et al.*, 1967:954). EL SALVADOR (Felten, 1957:153-155): Amate de Campo, La Paz; Finca Raquelina, Ahuachapan; Hacienda Nancuchiname, Usulután; Hacienda San Antonio, Sonsonate; Isla de la Cabra, Santa Ana; Laguna de Guija, Santa Ana; San Salvador, San Salvador. HONDURAS: El Zapote, Francisco Morazán (Goodwin, 1942:156).

Marginal records.—HONDURAS: San Pedro Sula. GUATEMALA: 3 mi. E Jocotán. EL SALVADOR: El Tablón; Lake Coatepeque; 10 mi. NW Santa Tecla; 1 mi. NW San Salvador; 6 mi. E San Salvador; Mt. Cacaguatique. HONDURAS: Monte Redondo; El Caliche Orica; Catacamas; Escuela Agricultura Panamericana. NICARAGUA: Quilalí; Savala; Santa Rosa, 17 km. N, 15 km. E Boaco; 1 km. N, 2½ km. W Villa Somoza; 2 km. N, 3 km. E Mérida, Isla de Ometepe. COSTA RICA: 9 km. N Liberia, 4 km. E Interamerican Highway; 1 7/10 mi. by road W Tilarán; 1 mi. N Santa Ana; *Los Higuerones*; Monte Rey, 22 km. S San José; Sabanilla de Pirrís; Boca del Barranca; San Juanillo hence northward along the coast. NICARAGUA: 3 mi. SE San Pablo; 14 km. S Boaco; 8 km. (by road) N Las Maderas; 9 mi. NNE Estelí. HONDURAS: La Piedra de Jesús. EL SALVADOR: Río Goascorán, 13° 30′ N; Pine Peaks, 3 mi. W Volcán Conchagua hence northward along the coast. GUATEMALA: Tiquisate; San Lucas; Sacapulas; La Primavera; ½ mi. N, 1 mi. E Salamá; *Río Santiago, 152 km. NE Guatemala City (17 mi. NE Río Hondo)*; Gualán.

Liomys salvini vulcani (J. A. Allen, 1908)

1908. *Heteromys vulcani* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 24:652, 13 October.
1946. *Liomys salvini vulcani*, Goodwin, Bull. Amer. Mus. Nat. Hist., 87:374, 31 December.

Holotype.—Adult female, skin and skull, AMNH 28315, from Volcán de Chinandega, about 4000 ft., Chinandega, Nicaragua; obtained on 7 May 1909 by W. B. Richardson. Skin in fair condition; skull in poor condition. The skull was broken in half between the orbits and subsequently was glued together; the left zygomatic arch is completely missing, the right zygomatic arch has the middle section missing, the tip of right nasal bone is missing as is the posterior portion of left dentary and the lower left third molar.

Measurements of holotype.—Total length, 220; length of tail, 110; length of hind foot, 25; interorbital constriction, 6.8; mastoid breadth, 13.5; length of nasals, 11.1; length of rostrum, 12.5; length of maxillary toothrow, 4.9; interparietal width, 8.4; interparietal length, 4.0.

Distribution.—This subspecies is confined to western Nicaragua—on the volcanos that make up the Cordillera los Marrabios and the lowland to the west of them, west of Lake Managua, on the Meseta de los Pueblos west of Lake Nicaragua, and on Isla de Zapatera (Fig. 40).

Comparisons.—From *Liomys salvini salvini*, the subspecies *vulcani* can be distinguished by its consistently smaller size in both external and cranial measurements (compare values for samples 15, 17 with those for 13, 14, 16, 20, 21 in Table 21). There does not appear to be any difference between the two subspecies in qualitative cranial characters.

Compared with *Liomys salvini crispus* of Oaxaca, Chiapas, and Guatemala, *Liomys salvini vulcani* averages longer in total length and length of tail, but smaller in measurements of the cranium such as greatest length of skull, zygomatic breadth, and depth of braincase (compare values of samples 15, 17 with those of samples 1-4 in Table 21). None of 45 specimens of *Liomys salvini crispus* for which data were recorded had the interparietal bone divided, whereas four individuals of 41 examined from sample 15, and 10 individuals of 81 examined from sample 17 (samples of *vulcani*) had the bone divided (Table 23). The two samples of *vulcani* have 29.3 and 14.6 per cent of the individuals with the posterior margin of the interparietal bone deeply notched, whereas the lowest percentage for *crispus* was 64.0 for sample 1 (see Table 23).

Remarks.—This small-sized subspecies is confined to lowlands of western Nicaragua and adjacent areas such as Cordillera los Marrabios, Meseta de los Pueblos, and Isla de Zapatera. J. A. Allen described *vulcani* as a full species in 1908 and it was recognized as such until Goodwin (1946:375) reduced *vulcani* to a subspecific status under *salvini* and assigned to it specimens from Guanacaste, Costa Rica. The name *vulcani* stood in the literature as a valid species for many years not because of its many unique characteristics, but because the type series was in poor condition and spiny pocket mice were unreported from elsewhere in Nicaragua. Not until field parties from The University of Kansas, under the aegis of a grant from the Army Research and Development Command, began collecting mammals in Nicaragua in 1964 did the widespread distribution of the species become apparent and delineation of the geographic range of *vulcani* become possible. It now appears that *L. s. vulcani* approaches the southern end of its distribution in the vicinity of La Calera (near Nandaime), Nicaragua, and that specimens from the Guanacaste region of Costa Rica formerly assigned to *vulcani* are best considered as representatives of *L. s. salvini.*

Many of the areas, such as northwest of Lake Managua in the vicinity of Larreynaga and the lowland between Lake Managua and Lake Nicaragua, in which intergradation between *vulcani* and *salvini* is suspected, unfortunately are unrepresented by specimens of spiny pocket mice at the present time. However, specimens from 8 km. N Las Maderas are clearly intergrades between *vulcani* and *salvini* and may indicate that *vulcani* occupies much of the lowland areas around Lake Managua and makes contact with *salvini* in the foothills of the Cordillera Central. The distribution of *L. s. vulcani* appears to extend eastward on the Meseta de los Pueblos to the south of Managua in the vicinity of Volcán de Mombacho on the northwestern edge of Lake Nicaragua, thereby interrupting the geographical range of *L. s. salvini* from east of Lake Nicaragua and southwestern Nicaragua and Costa Rica. (The significance of the interruption of the range of *L. s. salvini* is discussed more fully in the account of that subspecies.) No adult specimens are available from Hacienda Mecatepe, just to the south of Volcán de Mombacho, but two subadult males (KU 108195-96) that I would judge to be nearly adult size have small external and cranial measurements (total length, 210, 199; greatest length of skull, 31.0, 30.7), and appear to be referable to *vulcani*. The one specimen from Isla de Zapatera (KU 71222) available for measuring (the other is in alcohol) is a young animal, but it is small (greatest length of skull, 29.8) and I tentatively refer the population from the island to *vulcani* until adult material becomes available for study.

An adult male from La Calera, Nicaragua (KU 108197), has small external and cranial measurements (total length, 220; greatest length of skull, 31.4) and agrees well with typical specimens of *vulcani*. However, the one specimen from 3 mi. SE San Pablo, Rivas (adult male, KU 71223), only a few miles south of La Calera, is relatively large (total length, 237; greatest length of skull, 32.0) and, accordingly, has been referred to *salvini*. The zone of contact between these two races in the south is probably in the area between La Calera and San Pedro near the southern edge of the Meseta de los Pueblos.

Ten adult males and 10 nonpregnant, adult females from northwestern Nicaragua averaged, respectively, 14.2 (13.0-15.0) and 13.9 (12.0-16.0) for length of ear and 48.6 (36.0-60.5) and 37.1 (32.5-47.7) for weight.

Specimens examined (316).—NICARAGUA: 4½ km. N Cosigüina, 15 m., Chinandega, 10 (KU); 3 km. N, 4 km. W Diriamba, 600 m., Carazo, 28 (KU); 3 mi. SE El Crucero, Managua, 2 (KU); El Paraíso, 1 km. N Cosigüina, 20 m., Chinandega, 4 (KU); Hacienda Azacualpa, Managua, 7 (KU); Hacienda Bellavista, 720 m., Volcán Casita, 46 (28 KU, 18 UCLA); Hacienda Corpus Christi, Managua, 16 (USNM); Hacienda Cutirre, Volcán Mombacho, 1400 ft., Granada, 1 (UCLA); Hacienda Las Colinas, 4 mi. WNW Puerto Momotambo, León, 35 (8 KU, 2 UA, 25 USNM); Hacienda Mecatepe, Granada, 3 (KU); NW side Isla de Zapatera, Granada, 2 (KU); La Calera, Nandaime, 2 (KU); Lake Jiloa, Managua, 20 (AMNH); León, León, 1 (AMNH); 5 mi. NW Managua, Managua, 14 (KU); 4 mi. W Managua, Managua, 30 (KU); 3 mi. SW Managua, Managua, 67 (KU); 1 mi. SE Masachapa, *in* Carazo, 1 (KU); 1 mi. ENE Poneloya, León, 4 (KU); 2 mi. N Sabana Grande, Managua, 3 (KU); San Antonio, 35 m., Chinandega, 6 (KU); 6 mi. SE Tamarindo, León, 4 (KU); Volcán de Chinandega, Chinandega, 10 (AMNH).

Marginal records.—NICARAGUA: 4½ km. N Cosigüina; Volcán de Chinandega; Hacienda Bellavista, Volcán Casita; Hacienda Las Colinas, 4 mi. WNW Puerto Momotambo; Hacienda Corpus Christi; 2 mi. N Sabana Grande; Hacienda Cutirre, Volcán Mombacho; NW side Isla de Zapatera; La Calera, Nandaime; 1 mi. SE Masachapa.

Liomys adspersus

Panamanian Spiny Pocket Mouse

This species occupies a restricted geographic range in central Panamá. Specimens are available from as far west as Guabulá and as far east as Chepo. The species occurs mainly in the Pacific drainage, although it is known from several localities in the headwaters of the Caribbean drainage in the vicinity of the Canal Zone.

Diagnosis

External and cranial measurements large; premolars similar in structure to those of *L. salvini*; baculum with large rounded base, shaft oval to a point just posterior to the slightly upturned tip where it is dorsoventrally flattened; glans penis medium-sized in comparison with length of baculum, tip of glans short, glans highly sculptured and with deeply incised ventral folds; urethral lappets bilobed; 2N = 56; FN probably 84; head of spermatozoon short with bluntly rounded apex and distinct neck between head and midpiece; wings of pterygoids narrow; parasitized by the anopluran species *Fahrenholzia fairchildi*; six plantar tubercles; upper parts usually chocolate brown (some paler individuals may show grayish tones); no lateral stripe; underparts white; hairs on back curled upward so as to be conspicuous above spines.

Comparisons

For comparisons of *Liomys adspersus* with *L. irroratus*, *L. pictus*, *L. spectabilis*, and *L. salvini*, see the accounts of those species.

Ecology

Handley (1966:778) stated that *Liomys adspersus* was abundant in the semiarid savannah country of the Pacific coast of western and central Panamá where it was commonest in thorny scrub and weedy fields (see also Bole, 1937:164). An extensive field study of this species was conducted by Fleming (1969, 1970, 1971) in the Canal Zone. He found *adspersus* to be the commonest rodent in the Rodman forest with its population density ranging from 5.4 to 11.0 individuals per hectare. The average home range was 0.56 hectare with no significant difference between the size of the home range of males and females. Examination of stomach contents of more than 30 specimens revealed that these pocket mice fed on seeds, other plant material, and insects.

Geographic Variation

Univariate Analysis

Adult specimens from throughout the geographic range of *Liomys adspersus* were grouped in three samples for analysis. The samples were composed of specimens labeled with reference to the following locations (Fig. 41): *sample 1*—Canal Zone (Balboa, Fort Kobbe, Madden Road, Río Chágres, Summit) and Panama (Cerro Azul, Río Hato); *sample 2*—Panama (Sante Fé, San Fran-

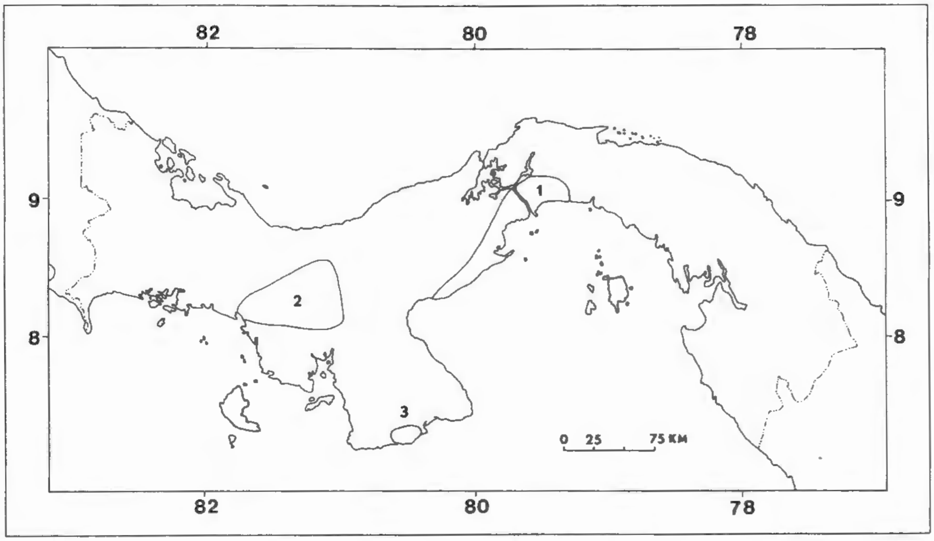


FIG. 41.—Approximate geographic areas included in the three samples of *Liomys adspersus*. See text for localities included in each sample.

cisco, Tolé); *sample 3*—PANAMA (Guánico). Table 27 gives standard statistics for the samples of *Liomys adspersus*.

External Measurements

Males from the Azuero Peninsula (3) and central Panamá (2) average greater in total length (Tables 27, 28) than do males from the Canal Zone (1). Females exhibit this same pattern, but specimens from sample 2 are somewhat larger than those from 3. For length of tail, (Tables 27, 28) males had two nonsignificant subsets—samples 3 and 2 and samples 2 and 1. Females also had two nonsignificant subsets but these are composed of samples 3 and 2 and a nonoverlapping subset of sample 1. No significant differences were found between the means for males for length of hind foot (Table 27). Females exhibited two overlapping subsets (Table 28) as follows: samples 2 and 3 and samples 3 and 1.

Cranial Measurements

No significant differences were found between the means of greatest length of skull for both males and females (Table 27). The means for males from samples 2 and 3 are a millimeter or more longer than those from sample 1, but for females the means are not especially different. Males and females both exhibit two overlapping nonsignificant subsets for zygomatic breadth (Table 28). However, for males sample 3 has the largest mean and sample 1 has the smallest mean, whereas for females the reverse is true.

Females show no significant differences between the means of the samples for the remaining eight cranial measurements (Table 27). For these measurements, females in sample 1 had the largest mean value for three (interorbital constriction,

TABLE 27.—*Geographic variation in external and cranial measurements among 3 samples of* Liomys adspersus. *See text for key to sample numbers.*

Sample number	Males N	Males Mean	Males Range	Males 2 SE	Females N	Females Mean	Females Range	Females 2 SE
				Total length				
1	9	249.6	232.0-264.0	7.30	10	238.6	222.0-264.0	8.18
2	2	265.0	264.0-266.0	2.00	5	253.2	247.0-265.0	6.46
3	18	265.9	248.0-285.0	5.29	6	249.7	244.0-264.0	5.99
				Length of tail				
1	9	119.9	107.0-130.0	6.05	10	118.2	109.0-130.0	3.83
2	2	130.0	127.0-133.0	6.00	5	127.8	124.0-131.0	2.93
3	18	136.6	123.0-148.0	3.37	6	128.8	124.0-138.0	4.54
				Length of hind foot				
1	9	29.9	27.0-32.5	1.09	14	29.5	28.0-31.0	0.62
2	5	30.6	29.0-32.0	1.36	5	30.8	30.0-32.0	0.75
3	21	31.4	26.0-34.0	0.74	8	30.6	29.0-32.0	0.92
				Greatest length of skull				
1	8	34.8	32.2-36.3	0.97	15	34.6	32.9-35.7	0.46
2	5	35.9	34.5-37.3	0.91	4	35.0	33.6-36.2	1.06
3	20	35.8	33.4-38.9	0.64	7	34.7	34.3-35.1	0.24
				Zygomatic breadth				
1	4	15.9	15.1-16.6	0.62	7	16.8	16.3-17.5	0.38
2	3	16.7	16.4-16.9	0.31	3	16.6	16.4-17.0	0.40
3	5	17.0	16.6-17.4	0.33	3	16.0	15.8-16.2	0.23
				Interorbital constriction				
1	10	7.5	7.1-7.8	0.14	16	7.6	7.0-8.2	0.18
2	5	7.6	7.4-8.1	0.25	4	7.5	7.1-7.8	0.30
3	21	7.4	7.0-8.0	0.12	8	7.5	7.3-7.8	0.12
				Mastoid breadth				
1	9	14.5	13.8-15.0	0.24	15	14.5	14.1-14.8	0.12
2	5	15.1	14.7-15.6	0.35	4	14.9	14.8-14.9	0.05
3	20	14.5	14.0-15.3	0.14	8	14.5	13.8-15.2	0.28
				Length of nasals				
1	10	14.1	12.8-15.0	0.45	16	14.0	13.0-15.2	0.31
2	5	14.5	13.7-15.3	0.57	4	14.2	13.6-15.0	0.61
3	20	15.1	13.9-17.3	0.31	7	14.1	13.5-14.8	0.32
				Length of rostrum				
1	8	15.7	15.0-16.4	0.44	13	15.5	14.5-16.3	0.26
2	5	16.0	15.2-16.8	0.56	3	15.4	14.6-16.0	0.85
3	14	16.1	15.0-17.9	0.44	5	15.2	14.7-15.5	0.29

TABLE 27.—*Continued.*

				Length of maxillary toothrow				
1	9	5.3	5.0-5.5	0.11	16	5.3	5.0-5.5	0.09
2	5	5.3	5.2-5.5	0.10	4	5.3	5.1-5.4	0.13
3	20	5.4	4.9-5.9	0.11	8	5.3	5.1-5.6	0.15
				Depth of braincase				
1	8	9.4	8.8-10.2	0.32	14	9.3	8.7-9.9	0.19
2	5	9.8	9.3-10.2	0.30	4	9.4	9.0-9.8	0.39
3	20	9.5	8.9-10.1	0.14	8	9.2	8.9-9.5	0.16
				Interparietal width				
1	6	8.6	8.0-9.2	0.36	14	8.5	7.7-9.2	0.23
2	5	8.3	7.7-9.3	0.64	4	8.5	7.8-9.6	0.83
3	15	8.2	7.2-8.9	0.22	8	8.1	7.5-8.5	0.30
				Interparietal length				
1	6	4.8	4.4-5.2	0.27	15	4.6	3.8-5.0	0.18
2	5	4.5	4.0-4.9	0.29	4	4.3	3.9-5.0	0.48
3	19	4.4	3.4-4.8	0.19	8	4.4	4.0-5.2	0.27

interparietal width, interparietal length), those of sample 2 had the largest value for four measurements (mastoid breadth, length of nasals, length of rostrum, and depth of braincase), and females from sample 3 averaged largest in one (length of maxillary toothrow).

Males exhibit significant differences between the sample means for mastoid breadth and length of nasals (Table 28), but not for the remaining six measurements. For mastoid breadth, sample 2 forms a subset distinct from samples 1 and 3. Two overlapping subsets are formed for length of nasals. Mice from each of the three samples averaged largest for two of the remaining six measurements (Table 27) as follows: sample 1, interparietal width and interparietal length; sample 2, interorbital constriction and depth of braincase; sample 3, length of rostrum and length of maxillary toothrow.

Qualitative Cranial Characters

Condition of interparietal bone (Table 29).—None of the specimens examined from the vicinity of the Canal Zone (1) have a divided interparietal bone. A relatively high percentage (27.3) of individuals from the Azuero Peninsula (3) do have the interparietal bone divided, and mice from the geographically intermediate sample (2) have an intermediate percentage (12.5) with the interparietal bone divided in half.

All three samples have a high percentage of individuals with the posterior margin of the interparietal bone notched.

Condition of posterior nasal region (Table 30).—All specimens examined had the posterior margin of the nasal bones truncate in shape. All individuals examined but two from sample 3 had the premaxillary bones longer than the nasal bones.

TABLE 28.—*Results of SS-STP analyses for those measurements of* Liomys adspersus *for which there was found to be a significant difference between the sample means. Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
		Total length			
3	265.9		2	253.2	
2	265.0		3	249.7	
1	249.6		1	238.6	
		Length of tail			
3	136.6		3	128.8	
2	130.0		2	127.8	
1	119.9		1	118.2	
		Length of hind foot			
			2	30.8	
			3	30.6	
			1	29.5	
		Zygomatic breadth			
3	17.0		1	16.8	
2	16.7		2	16.6	
1	15.9		3	16.0	
		Mastoid breadth			
2	15.1				
1	14.5				
3	14.5				
		Length of nasals			
3	15.1				
2	14.5				
1	14.1				

TABLE 29.—*Geographical variation in the configuration of the interparietal bone of* Liomys adspersus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Interparietal bone			Posterior margin of interparietal bone			
Sample	N	Undivided	Divided	N	Notched	Slightly notched	Unnotched
1	20	100.0	0	21	81.0	14.3	4.7
2	8	87.5	12.5	8	75.0	25.0	0
3	22	72.7	27.3	27	66.7	22.2	11.1

TABLE 30.—*Geographical variation in bones of the posterior portion of the nasal-premaxillary complex of* Liomys adspersus. *Figures are given in per cent of total number for each sample. See text for key to sample numbers.*

	Shape of posterior margin of nasals				Length of premaxillary bones		
Sample	N	Emarginate	Rounded	Truncate	N	Longer then nasals	Equal to nasals
1	22	0	0	100.0	22	100.0	0
2	8	0	0	100.0	8	100.0	0
3	27	0	0	100.0	27	92.6	7.4

Multivariate Analysis

Means of the 13 external and cranial measurements and four qualitative cranial characters were used in the NT-SYS multivariate analysis program. The three samples of *Liomys adspersus* were analyzed along with the 21 samples of *Liomys salvini* so that the relationship of these two species could be studied. Distance and correlation matrices were generated for both males and females from which phenograms were prepared. The distance phenograms are presented in Fig. 42. The first three principal components were computed from a matrix of correlation among the 17 characters; these first three components combine to express 79.89 per cent of the phenetic variation in males and 81.99 per cent in females.

Distance coefficients between samples of male *Liomys adspersus* were as follows: between 1 and 2, 0.837; between 2 and 3, 0.735; and between 1 and 3, 1.094. The same values for samples of females were 0.643, 0.687, and 0.860. The distance between these three samples (in numerical order) and the nearest sample of *Liomys salvini* (sample 21) were for males and females, respectively, 1.489, 1.613, 1.968, 1.762, 1.975, and 1.574.

The distance phenogram (Fig. 42) shows the three samples of *Liomys adspersus* "distantly" separated from samples of *Liomys salvini.* Within the cluster of *adspersus* samples, sample 1 is phenetically most distinct for males and sample 3 for females.

In the principal component analysis, the amount of phenetic variation expressed in the first three components for male and female *Liomys adspersus* and *Liomys salvini,* respectively, was 60.26 and 61.51 per cent for component I, 13.90 and 13.75 per cent for component II, and 5.74 and 6.72 per cent for component III. On the three-dimensional plots (Figs. 43, 44), it can be seen that the three samples of *L. adspersus* are separated by a considerable "distance" along the first principal component from the samples of *L. salvini.* This component expresses most of the phenetic variation and is most heavily influenced by size. Sample 1 of *Liomys adspersus* is somewhat removed from the other two samples along the first principal component for males, but for females the three samples are grouped near each other.

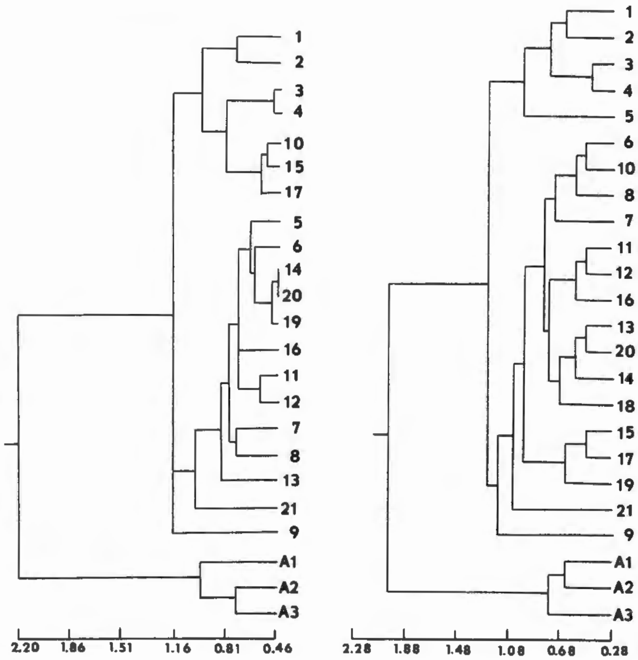


FIG. 42.—Phenograms of numbered samples (see Figs. 31 and 41 and text) of *Liomys adspersus* (labeled A1, A2, and A3) and *Liomys salvini* (males left, females right) computed from distance matrices based on standardized characters and cluster by unweighted pair-group method using arithmetic averages (UPMGA). The cophenetic correlation coefficient for the phenogram for males is 0.917 and for females is 0.913.

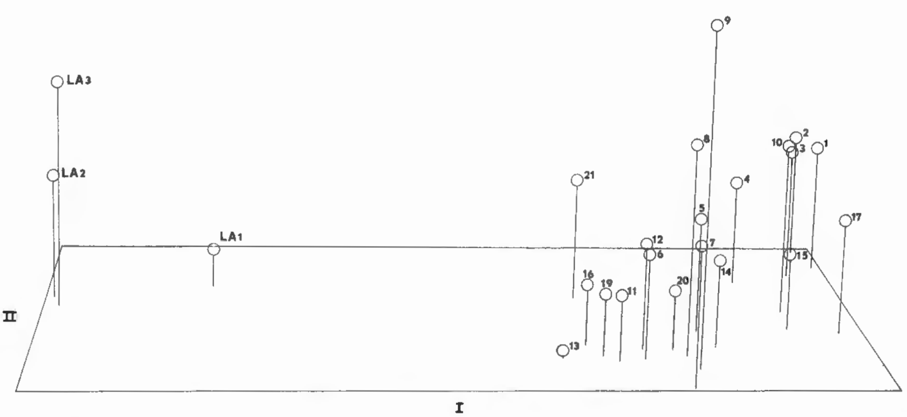


FIG. 43.—Three-dimensional projection of three samples of male *Liomys adspersus* (labeled LA1, LA2, and LA3) and 20 samples of *Liomys salvini* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Figs. 31 and 41 and text for key to samples.

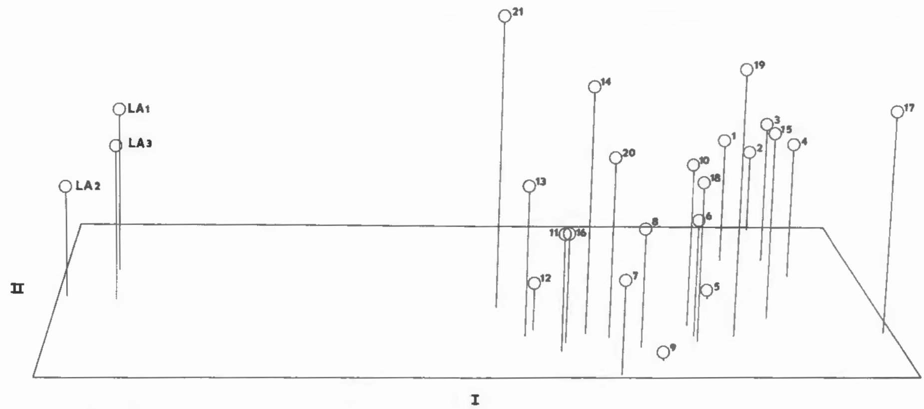


FIG. 44.—Three-dimensional projection of three samples of female *Liomys adspersus* (labeled LA1, LA2, and LA3) and 21 samples of *Liomys salvini* onto the first three principal components based upon a matrix of correlation among the 13 external and cranial measurements and four qualitative cranial characters. Components I and II are indicated in the figure and component III is represented by height. See Figs. 31 and 41 and text for key to samples.

Variation in Color

Only two samples of *Liomys adspersus* were available for color analysis. Color reflectance readings for the samples from the Canal Zone and the Azuero Peninsula, respectively, were as follows: red reflectance, 9.8 and 10.3; green reflectance, 5.8 and 5.7; blue reflectance, 5.2 and 5.6. None of the means for the three reflectances were found to be significantly different using the Student's *t*-test. These two samples are paler than the sample of *Liomys salvini* from the vicinity of San José, Costa Rica, and more nearly resemble the sample from the Guanacaste of Costa Rica (see Table 26).

Taxonomic Conclusions

From the results of the univariate and multivariate analyses, and the data presented in the section on specific relationships, it is clear that *Liomys adspersus* is a species closely related to *Liomys salvini* of more northern regions of Central America. Within *adspersus* there appears to be little geographic variation, and I therefore consider it to be a monotypic species.

Liomys adspersus (Peters, 1874)

1874. *Heteromys adspersus* Peters, Monotsb. preuss. Akad. Wiss., Berlin, p. 357, May.
1911. *Liomys adspersus*, Goldman, N. Amer. Fauna, 34:51, 7 September.

Holotype.—Young adult male, mounted skin with skull, unknown number in Berlin Museum, from Panamá. The type locality was restricted to the City of Panamá by Goldman (1920:118).

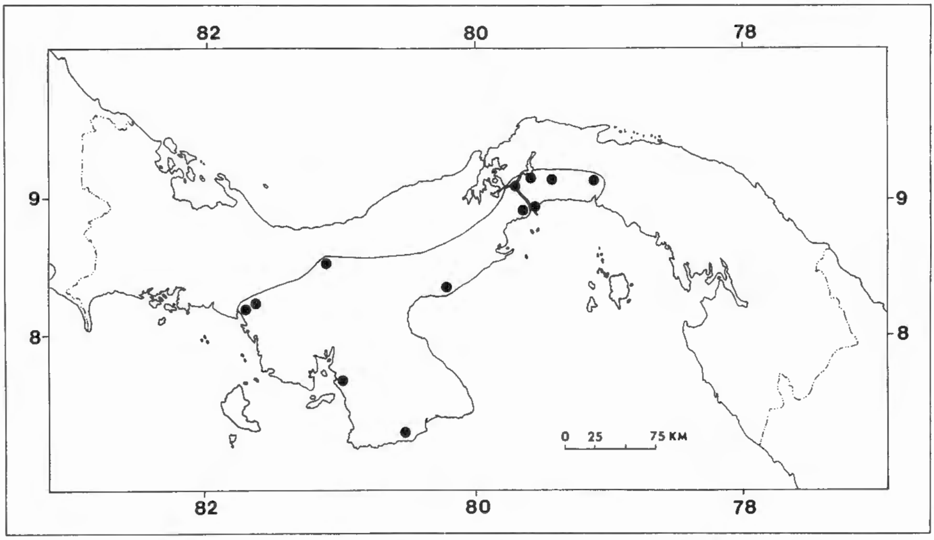


FIG. 45.—Geographic distribution of *Liomys adspersus* in Panamá.

Measurements of holotype.—(From original description) total length, 240; length of tail, 95; length of hind foot, 30.

Distribution.—Central Panamá principally on the Pacific versant (Fig. 45).

Comparisons.—See above.

Remarks.—Although I have not seen the holotype of this species, which is from an unknown locality in Panamá, Peters (1874) presented an excellent plate showing the cranium, toothrows, feet, ear, and head of this specimen. Clearly from these figures the specimen is a young adult of the genus *Liomys.*

The geographic distribution of *Liomys adspersus* appears to lie mainly in the semiarid savannahs of the Pacific drainage of central and western Panamá. However, a few specimens from Summit, Empire, Buenos Aires, Juan Mina, Río Chágres, and the Cacao Plantation near Gamboa are from the headwaters of Caribbean drainage in the vicinity of the Canal Zone. What effect construction of the canal has had upon the distribution of these mice can only be a matter of conjecture. The species, *Liomys salvini*, that is geographically nearest *adspersus* is also its nearest relative within the genus; the ranges of the two species presently are separated by a distance of approximately 300 kilometers.

What little significant variation that is present among samples of this species is mainly for external measurements, which may be the result of variation in techniques of collectors rather than the mice. In cranial measurements, all taken by myself, significant differences among the means of samples were found only in zygomatic breadth, mastoid breadth, and length of nasals for males, and in zygomatic breadth for females. Basically there is little variation among the mice of this species.

Mean length of ear for 10 males and 10 females from west-central Panamá was, respectively, 15.1 (12.0-17.0) and 14.6 (12.0-16.0). The same individuals (females not pregnant) averaged, respectively, 77.7 (65.0-92.0) and 57.4 (49.0-66.0) for weight.

Specimens examined (194).—CANAL ZONE: Albrook Air Force Base, 1 (USNM); 2 mi. N Albrook Field, 1 (USNM); Albrook Res., 4 (USNM); Balboa, 3 (FMNH); Chiva Chiva, 1 (USNM); Cocoli, 1 (USNM); Corozal, 1 (USNM); Curundu, 1 (USNM); Empire, 2 (USNM); Farfan, 1 (USNM); Fort Clayton, 6 (USNM); Fort Kobbe, 14 (USNM); Juan Mina, 1 (UA); Madden Forest, 1 (USNM); Madden Road, 6 (USNM); Río Chágres, 4 (AMNH); Summit, 4 (3 USNM, 1 MCZ).

PANAMA: 2 km. NE Buenos Aires, Panamá, 8 (KU); Cerro Azul, Panamá, 3 (USNM); Chepo, Panamá, 1 (USNM); 1 mi. N Guabalá, Chiriqui, 1 (USNM); Guanico, Los Santos, 95 (USNM); Las Cumbres, 7 km. N, 2 km. W Pueblo Nuevo, Panamá, 1 (KU); 1½ mi. E Montijo Bay [probably about 1 mi. E Paracoté], Veraguas, 1 (UMMZ); Paracoté, Veraguas, 1 (UMMZ); 2 mi. E Río Hato, Cocle, 10 (USNM); Río Santa María, Santa Fé, Veraguas, 17 (USNM); 2 mi. S San Francisco, 200 ft., Veraguas, 1 (TCWC); 2 mi. NE Tolé, 1000 ft., Chiriqui, 3 (USNM).

Additional records.—CANAL ZONE: Cacao Plantation (Brennan and Yunker, 1966:243); Corte Culebra Road (Brennan and Yunker, 1966:254); Experimental Gardens, near Summit (Enders, 1935:451); Nuevo Emperador (Brennan and Yunker, 1966:248); Rodman Naval Ammunition Depot (Fleming, 1970:476; 1971:16).

Marginal records.—PANAMA: Cerro Azul; Chepo. CANAL ZONE: Balboa; Fort Kobbe. PANAMA: Río Hato; Guánico; Paracoté; Guabalá; 2 mi. NE Tolé; Río Santa María, Santa Fé. CANAL ZONE: Río Chágres; *Juan Mina*. PANAMA: 2 km. NE Buenos Aires.

Status of **Liomys centralis**

The species *Liomys centralis* was described by Hibbard (1941*a*:349-350, 1941*b*:277) from the Rexroad Fauna (locality no. 3) of the Upper Pliocene of southwestern Kansas. The material upon which this taxon is based consists of part of the left ramus bearing incisor, p4, ml, and the alveolus of m2 (KUMVP 4589). My study of this specimen and specimens of the five Recent species of the genus *Liomys* has led to the conclusion that *centralis* is not a member of the genus *Liomys* and almost without a doubt it is not even in the lineage leading to the genus. I have based this conclusion upon the following differences between *centralis* and Recent members of the genus: 1) the metalophid of p4 of *centralis* is composed of three fairly distinct cusps, whereas Recent specimens show no more than two cusps in this lophid; 2) in *centralis* the middle cusp of the metalophid of p4 is connected across the rather shallow median valley to one of the accessory cusps in the protolophid (see Hibbard, 1941*a*:350 for a figure of this tooth), whereas in Recent species the median valley between the protolophid and metalophid is deep and there is never a connection between them across the middle of the tooth; 3) as pointed out by Hibbard (1941*a*:350, 1941*b*:277) the first wear pattern on the p4 of *centralis* will be H-shaped, whereas in all Recent species the two lophids first meet at their labial margins giving a C-shaped pattern of wear, but never one of H-shape; 4) the cusps on the molar of *centralis* must be higher and more distinct than in Recent species of *Liomys* because on *centralis* the cusps are still easily discernable with the permanent premolar in place, whereas in Recent specimens the cusps are only discernable in extremely young individuals with unworn molars (by the time the permanent premolar is in place the two lophids have been reduced to crescentic lakes of dentine separated by the enamel median valley); 5) on the molar of *centralis* there is no trace of an anterior cingulum, whereas this cingulum is visible on specimens of *Liomys* that are still unworn enough that the cusp pattern is evident; and 6) Hibbard (1941*a*:350, 1941*b*:277) believed that the molar of *centralis* would have an H-shaped wear pattern for a short time (this is a point on which I am uncertain based upon my examination of the specimen), whereas in all Recent species of *Liomys* the two lophids of the molars meet first at their labial margins, resulting in a C-shaped wear pattern (never an H-shaped pattern).

In considering trends in the evolution of the Heteromyinae (Wood, 1935), development of a connection between the metalophid and protolophid of the p4 across the middle of the tooth that would give an H-shaped wear pattern precludes "*Liomys*" *centralis* from the ancestry of the Recent species of *Liomys*, even though there are some similarities in structure of the protolophid of p4. When more is known about the evolutionary history of the Heteromyidae, I would not be surprised to find that "*Liomys*" *centralis* is more closely related to the Perognathinae lineage than to the Heteromyinae. However, for the present study it suffices to say that the species described as *Liomys centralis* is not a *Liomys*.

[Since this manuscript was submitted for publication, Hibbard (Bull. Amer. Mus. Nat. Hist., 148:88-90, 1972) has assigned *Liomys centralis* to the genus *Prodipodomys*. He considered it to be a distinct species, *Prodipodomys centralis*.]

SPECIFIC RELATIONSHIPS

In this section, the relationships among the five species of *Liomys* recognized in the previous section are discussed based upon 12 morphological and biological characteristics. Also, the relationships of these species to members of the genus *Heteromys* are examined. In most cases, I have used specimens of *Heteromys desmarestianus* as representatives of the genus, mainly because these were more readily available and more numerous in collections than were other species of *Heteromys.* I have used specimens of *Heteromys lepturus* and *Heteromys gaumeri* when *desmarestianus* was not available.

Anatomical characters studied include external and cranial measurements, structure of the unworn permanent premolars and molars, wear pattern of molars, bacula, glans penes, karyotypes, head and neck structure of spermatozoa, morphology of soles of hind feet, structure of pterygoid region, and characters of pelage. Biological characteristics that have been investigated include ecological preferences, reproductive patterns, and ectoparasite faunas. Each of these characters has been analyzed separately and the relationships as revealed by the character presented. In the final section of this work, a picture of the overall evolutionary and zoogeographic relationships of the species of *Liomys* and *Heteromys desmarestianus* will be presented.

External and Cranial Morphology

The external and cranial morphology of the species of *Liomys* and of *Heteromys* have been compared using ratio diagrams and discriminant function analyses. Pair-wise comparisons of the species of *Liomys* have been made for those pairs that were of interest because their geographic distributions are sympatric, or nearly so, and for those pairs that were judged to be closely related systematically. The five species of *Liomys* were compared with *Heteromys desmarestianus* and *Heteromys gaumeri.* Crania of the species of *Liomys* and of *Heteromys desmarestianus* are shown in Figs. 46 and 47.

In the ratio diagrams that follow, a sample that has a smaller mean for a given measurement than the standard will have a negative value and one that has a larger mean than the standard will have a positive value. Theoretically, a species having values that are correlated with the standard, but is either larger or smaller than the standard, will form a line parallel to the standard on the appropriate side. Therefore, fluctuations in the line of the test sample can be interpreted as proportional as well as absolute differences in size from the standard. In the discriminant function analyses, those characters with the smallest within-groups variance and largest between-groups variance will have the largest discriminant multipliers, and those measurements with the largest within-groups variance and smallest between-groups variance will have the lowest discriminant multipliers. Negative and positive values for the multipliers indicate proportional differences between the measurements.

Liomys pictus and *Liomys irroratus*

These two species occur sympatrically from north-central Jalisco southward to the Sierra Madre del Sur of Oaxaca. In this region, *L. pictus* occurs mainly in

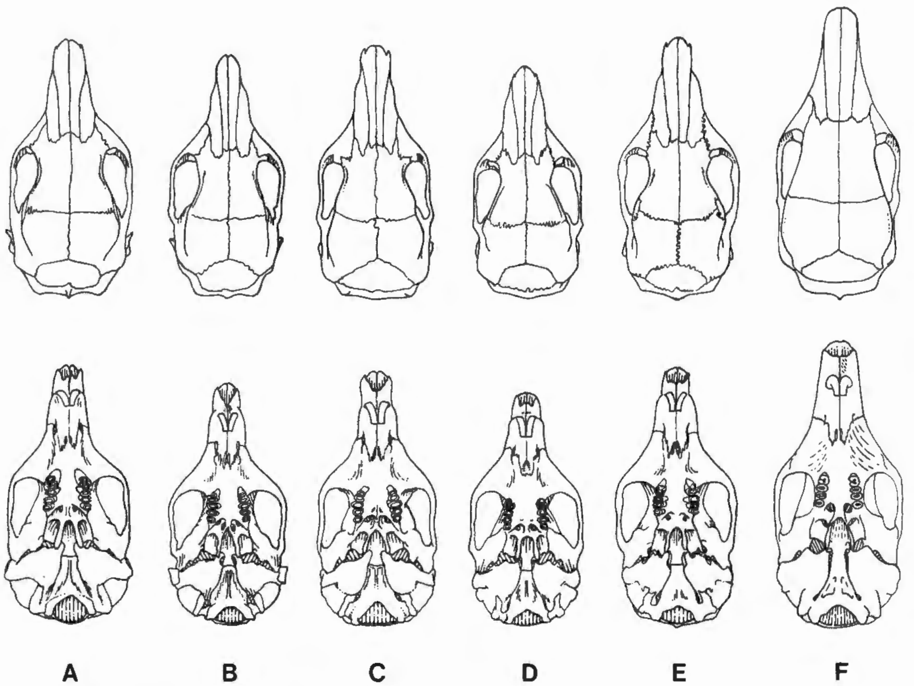


FIG. 46.—Dorsal and ventral views of the crania of five species of *Liomys* and one of *Heteromys*. The species are as follows: A, *Liomys irroratus irroratus* (KU 68855, ♂, 3 mi. W Mitla, Oaxaca); B, *Liomys pictus pictus* (KU 112276, ♂, San Sebastián, Jalisco); C, *Liomys spectabilis* (KU 96051, ♂, 2 2/10 mi. NE Contla, Jalisco); D, *Liomys salvini salvini* (KU 65042, ♂, 2 3/10 mi. W, 1/4 mi. N Iztapa, Escuintla, Guatemala); E, *Liomys adspersus* (KU 121528, ♂, 2 km. NE Buenos Aires, Panamá); F, *Heteromys desmarestianus desmarestianus* (KU 95037, ♂, 7 1/2 mi. NW Pueblo Nuevo, Chiapas). The scale at the lower right is 10 millimeters long.

lowland areas of the Pacific coast and Pacific slopes of the coastal mountains, but also occurs inland, to varying degrees, depending upon the geographic area (see Fig. 28). *Liomys irroratus*, on the other hand, occurs on the Mexican Plateau and adjacent areas of interior México. Although the two species are sympatric over a relatively large area, they are generally microallopatric (Smith, 1965:57).

In overall size, specimens of *L. irroratus* generally are larger than individuals of *pictus,* although this was not always the case as will be seen in some of the following examples. I have selected four areas where *irroratus* and *pictus* were actually or potentially microsympatric to analyze the relationship of the two species based upon their external and cranial morphology and to test for the presence of hybrids.

One sample was from southeastern Jalisco in the vicinities of Ciudad Guzmán and Contla and consisted of specimens of *Liomys pictus plantinarensis* and *Liomys irroratus jaliscensis*. In this area, *irroratus* appears to be uniformly larger than *pictus* in all measurements except interparietal width and interparietal length (Table 31); thus, the interparietal bone is proportionally larger in *pictus* than in

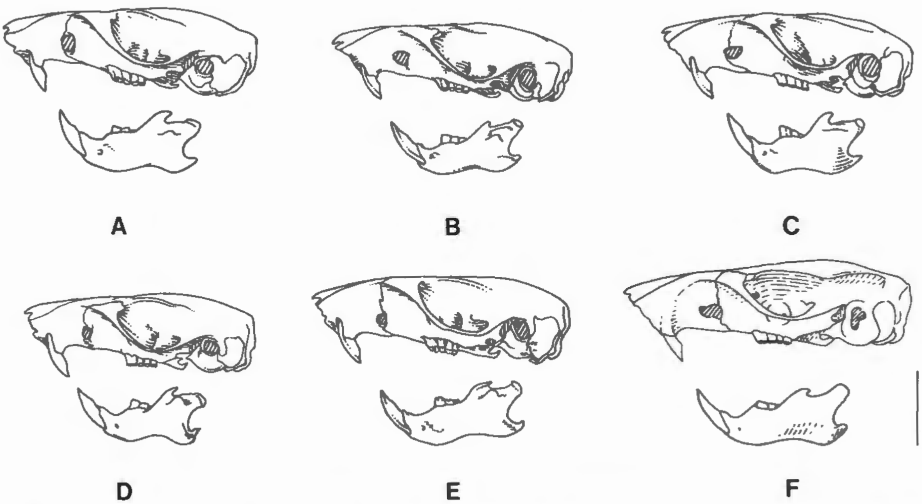


FIG. 47.—Lateral view of the crania and mandibles of five species of *Liomys* and one of *Heteromys*. The species are as follows: A, *Liomys irroratus irroratus* (KU 68855); B, *Liomys pictus pictus* (KU 112276); C, *Liomys spectabilis* (KU 96051); D, *Liomys salvini salvini* (KU 65042); E, *Liomys adspersus* (KU 121528); F, *Heteromys desmarestianus desmarestianus* (KU 95037). The scale at the lower right is 10 millimeters long.

irroratus. Mastoid breadth and depth of braincase were the measurements with the largest discriminant multipliers and among those with high discriminant scores. Other measurements with high discriminant multipliers and scores were length of hind foot, zygomatic breadth, and interorbital constriction. There was no overlap in the range of the discriminant scores of the two species from this area of Jalisco, but the ranges are separated only by a score of 0.32.

A second set of samples of *L. pictus* and *L. irroratus* was drawn from the area between Chilpancingo and Acapulco, Guerrero. In these samples, *irroratus* averaged larger than *pictus* in external measurements, whereas *pictus* averaged larger in most cranial measurements (Table 31). The two cranial measurements in which *irroratus* averaged larger than *pictus* were length of rostrum and depth of braincase; both of these measurements have high positive discriminant multipliers and scores. Greatest length of skull, interorbital constriction, and length of nasals had high negative discriminant multipliers. The nasals of *pictus* were found to be actually and proportionally longer than in *irroratus* (actually 0.8 millimeters longer and 39.9 per cent of greatest length of skull in *pictus* as compared with 37.9 per cent in *irroratus*), whereas in the other measurement of this portion of the skull, length of rostrum, *irroratus* was found to average very slightly larger and therefore proportionally longer (44.1 per cent of greatest length of skull in *pictus* as compared with 44.7 in *irroratus*). The range of discriminant scores of *L. pictus* from along the Pacific slope of the Sierra Madre del Sur of Guerrero was −8.71 to −5.49 and for *L. irroratus* was −3.51 to 0.82, giving a separation of 1.98. None of the specimens in this sample indicate hybridization between the two species.

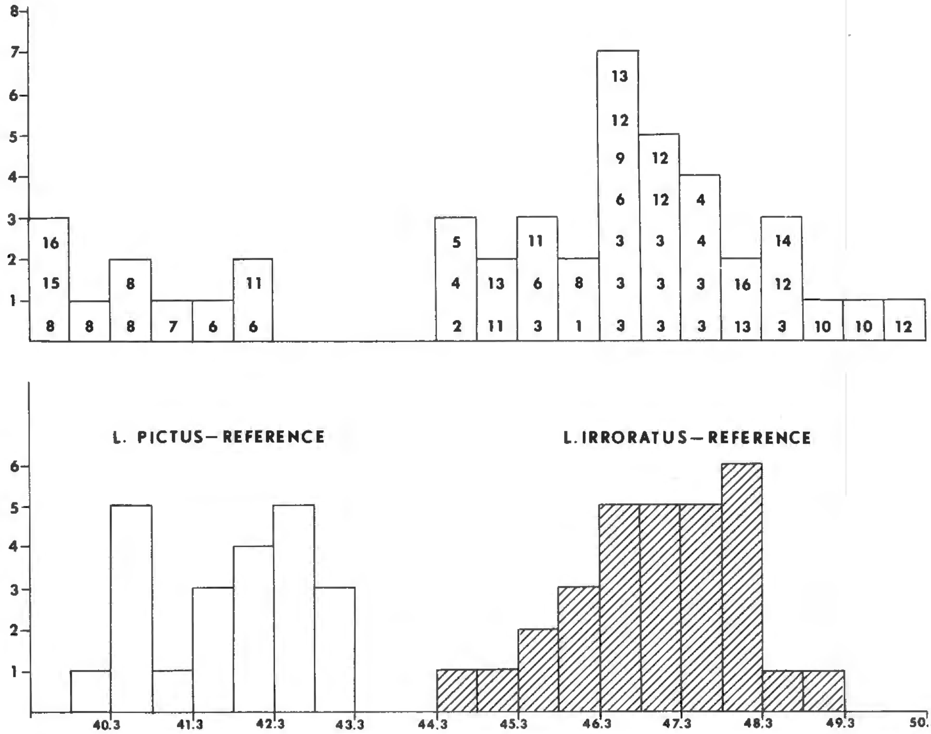


FIG. 48.—Histogram of linear discriminant scores based on a discriminant function analysis comparing *Liomys pictus plantinarensis* from Michoacán and Guerrero (sample 16 in analysis of geographic variation) and *Liomys irroratus torridus* from central Guerrero (sample 17 in analysis of geographic variation). Discriminant scores are indicated along the bottom of the histogram and frequency of individuals is indicated on the left-hand side. Individuals arranged below are from reference samples of *pictus*, at left, and *irroratus*, at right. Individuals arranged above are from the test sample; numbers, indicating the place of origin of test individual, are identified as follows: (1) Huajuapan, Oaxaca (holotype of *L. irroratus minor*); (2) 15 km. NNE Iguala, Guerrero; (3) Texcalzintla, 6 km. NNW Teloloapan, Guerrero; (4) 1 km. SSE Texcalzintla, Guerrero; (5) 4 3/10 km. N Teloloapan, Guerrero; (6) 2 km. ENE Los Sabinos, Guerrero; (7) Los Sabinos, Guerrero; (8) Iguala, Guerrero; (9) Teloloapan, Guerrero; (10) La Cofradia, Teloloapan, Guerrero; (11) 3200 m. SSE Iguala, Guerrero; (12) 1 km. NW Chapa, Guerrero; (13) Ojo de Agua de Chapa, 5 km. SE Teloloapan, Guerrero; (14) Chapa, Guerrero; (15) 2 1/2 mi. W Mexcala, Guerrero; (16) 1 1/2 mi. SE Zumpango, Guerrero.

A discriminant function analysis (Table 31) was performed upon a reference sample of *pictus* from Michoacán and Guerrero (specimens in sample 16 for analysis of geographic variation) and a reference sample of *irroratus* from the vicinity of Chilpancingo, Guerrero (sample 17 of geographic variation analysis). Onto the discriminant multipliers generated by this analysis were projected the measurements of specimens of both *pictus* (sample 17) and *irroratus* (sample 16) from the vicinity of Iguala, Guerrero, in the Balsas Basin (Fig. 48). Specimens of *L. irroratus* in the reference sample averaged larger than those of *pictus* in all

TABLE 31.—*Multipliers and scores resulting from discriminant function analyses comparing* Liomys pictus *and* Liomys irroratus *from four geographic areas.*

Measurements	Discriminant multiplier	*L. pictus* Mean	*L. pictus* Mean discriminant score	*L. irroratus* Mean	*L. irroratus* Mean discriminant score
Southeastern Jalisco					
Total length	−0.069	216.07	−14.91	231.19	−15.95
Length of tail	0.054	107.00	5.78	115.82	6.25
Length of hind foot	0.668	25.90	17.30	28.53	19.06
Greatest length of skull	−0.243	30.29	− 7.36	31.86	− 7.74
Zygomatic breadth	0.736	14.17	10.43	15.45	11.37
Interorbital constriction	0.823	7.30	6.01	7.90	6.50
Mastoid breadth	1.306	13.57	17.72	14.44	18.86
Length of nasals	−0.147	11.66	− 1.71	12.27	− 1.80
Length of rostrum	−0.046	13.01	− 0.60	13.98	− 0.64
Length of maxillary toothrow	−0.731	4.90	− 3.58	5.10	− 3.73
Depth of braincase	1.709	8.08	13.81	8.69	14.85
Interparietal width	−0.393	8.40	− 3.30	8.59	− 3.38
Interparietal length	−0.820	3.76	− 3.08	3.61	− 2.96
Total mean discriminant score			36.51		40.69
Range of discriminant scores			(34.01-38.37)		(38.69-43.18)
Pacific slope of Sierra Madre del Sur of Guerrero					
Total length	0.014	241.21	3.38	247.48	3.46
Length of tail	0.153	119.00	18.21	127.66	19.53
Length of hind foot	0.114	27.86	3.18	28.66	3.27
Greatest length of skull	−1.106	32.82	−36.30	32.44	−35.88
Interorbital constriction	−2.099	7.91	−16.60	7.72	−16.20
Mastoid breadth	−0.902	14.60	−13.17	14.55	−13.12
Length of nasals	−2.714	13.11	−35.58	12.31	−33.41
Length of rostrum	3.564	14.46	51.54	14.50	51.68
Length of maxillary toothrow	0.705	5.08	3.58	5.09	3.59
Depth of braincase	1.669	8.60	14.35	8.75	14.60
Interparietal width	0.020	8.61	0.17	8.29	0.16
Interparietal length	0.096	4.13	0.40	3.86	0.37
Total mean discriminant score			−6.84		− 1.95
Range of discriminant scores			(− 8.71 to − 5.49)		(−3.51 to 0.82)

TABLE 31.—*Continued.*

	Interior Michoacán and Guerrero				
Total length	−0.036	216.36	−7.79	246.90	−8.89
Length of tail	0.084	109.86	9.23	127.63	10.72
Length of hind foot	0.469	25.21	11.82	28.53	13.38
Greatest length of skull	0.388	29.80	11.56	32.40	12.57
Interorbital constriction	0.971	6.96	6.76	7.69	7.47
Mastoid breadth	−0.087	13.46	−1.17	14.50	−1.26
Length of nasals	−0.620	11.39	−7.06	12.38	−7.68
Length of rostrum	−0.138	12.89	−1.78	13.98	−1.93
Length of maxillary toothrow	0.233	4.83	1.13	5.09	1.19
Depth of braincase	2.827	7.99	22.59	8.74	24.71
Interparietal width	−0.734	8.27	−6.07	8.30	−6.09
Interparietal length	0.766	3.58	2.74	3.88	2.97
Total mean discriminant score			41.96		47.16
Range of discriminant scores			(40.24-43.26)		(44.63-49.14)
	Sierra Madre del Sur of Oaxaca				
Total length	0.016	253.50	4.06	266.89	4.27
Length of tail	0.051	130.77	6.67	143.92	7.34
Length of hind foot	0.203	29.98	6.09	32.65	6.63
Greatest length of skull	−0.187	33.85	−6.33	33.64	−6.29
Zygomatic breadth	−0.200	15.61	−3.12	15.92	−3.18
Interorbital constriction	1.490	7.89	11.76	8.14	12.13
Mastoid breadth	1.445	14.37	20.76	15.00	21.68
Length of nasals	−1.403	13.91	−19.52	13.00	−18.24
Length of rostrum	−0.770	15.22	−11.72	15.14	−11.66
Length of maxillary toothrow	−0.969	5.16	−5.00	5.38	−5.21
Depth of braincase	2.866	8.83	25.31	9.12	26.14
Interparietal width	−1.328	9.12	−12.11	8.50	−11.29
Interparietal length	−1.751	4.58	−8.02	3.99	−6.99
Total mean discriminant score			8.83		15.33
Range of discriminant scores			(6.86-10.85)		(12.90-17.34)

measurements, and only in interparietal width did the mean for *pictus* approach that for *irroratus*. Depth of braincase had by far the largest discriminant multiplier; other measurements with high positive discriminant multipliers were interorbital constriction, interparietal length, and length of hind foot. Length of nasals and interparietal width had relatively high negative discriminant multipliers. The range of discriminant scores for the *L. pictus* reference sample was 40.24 to 43.26 and for *L. irroratus* was 44.63 to 49.14, giving a separation of 1.37 between the two reference samples. Specimens tentatively identified as *L. pictus* from the Balsas Basin had a range of discriminant scores from 39.30 to 42.13 and those of *L. irroratus* ranged from 44.41 to 50.29. The specimen with the value of 44.41 has extremely small external measurements, which probably are erroneous. The next lowest score for *irroratus* was 44.72. I find no indication of hybridization between *L. pictus* and *L. irroratus* in the region of the Balsas Basin and the two have been taken together at four (6, 8, 11, and 16 on Fig. 48) localities there. A specimen of particular interest is the holotype of *L. i. minor* from Huajuapan, Oaxaca. Hooper and Handley (1948:13-14) suggested that this specimen resembled *Liomys pictus* in some characters, but my analysis clearly shows it to be a representative of *irroratus*.

The fourth area from which samples of *L. pictus* and *L. irroratus* were studied using discriminant functions was the mountains of the Sierra Madre del Sur of Oaxaca (samples 22, 23 for *pictus* and 16 for *irroratus* in the analysis of geographic variation). In this area, specimens of *irroratus* averaged larger than those of *pictus* in external measurements, and in all cranial breadth measurements except interparietal width and depth of braincase. Specimens of *L. pictus* averaged longer in all measurements of cranial length except for that of maxillary toothrow. Thus, the skulls of *pictus* in this area are longer and narrower than those of *irroratus*, and *irroratus* has a proportionally longer toothrow and a proportionally narrower interparietal bone. Measurements with high positive discriminant multipliers are interorbital constriction, mastoid breadth, and depth of braincase, and those with high negative multipliers are length of nasals, length of maxillary toothrow, interparietal width, and interparietal length. The range of discriminant scores for the *pictus* reference sample was 6.86 to 10.85 and for the *irroratus* reference sample was 12.90 to 17.34, giving a separation of 2.05.

In all four geographic areas analyzed the two species, *pictus* and *irroratus*, were separated on the basis of external and cranial measurements using a discriminant function analysis. No single or subset of measurements would consistently separate the two, although in all four tests depth of braincase and interorbital constriction had high discriminant multipliers. These data indicate that in order to differentiate these two species in western México on the basis of external and cranial measurements, it is necessary to study specimens in detail in each local area where they occur sympatrically.

Liomys irroratus and *Liomys spectabilis*

These two species have never been taken in the same traplines, but their geographic ranges do closely approach each other. All of the available adults with complete measurements of *Liomys spectabilis* and a sample of *Liomys irroratus* from the vicinity of the range of *spectabilis* in southeastern Jalisco were compared using discriminant functions (Table 32). Measurements of total length and length of tail were not used because many specimens of *spectabilis* lacked complete tails.

L spectabilis averaged larger than *L. irroratus* in all measurements except for interparietal width (in which the averages were the same), and depth of braincase (in which *irroratus* averaged 0.25 millimeters larger). Length of rostrum and interparietal length had high positive discriminant multipliers and depth of braincase, interorbital constriction, and zygomatic breadth had high negative multi-

TABLE 32.—*Multipliers and scores resulting from a discriminant function analysis between* Liomys spectabilis *and* Liomys irroratus *from southeastern Jalisco.*

Measurements	Discriminant multiplier	L. spectabilis Mean	L. spectabilis Mean discriminant score	L. irroratus Mean	L. irroratus Mean discriminant score
Length of hind foot	−0.007	30.46	− 0.21	28.53	− 0.20
Greatest length of skull	−0.129	34.16	− 4.41	31.86	− 4.11
Zygomatic breadth	−0.882	15.65	−13.80	15.45	−13.63
Interorbital constriction	−0.801	7.98	− 6.39	7.90	− 6.33
Mastoid breadth	0.260	14.58	3.79	14.44	3.75
Length of nasals	0.253	13.63	3.45	12.27	3.10
Length of rostrum	2.074	15.52	32.19	13.98	28.99
Length of maxillary toothrow	−0.172	5.25	− 0.90	5.10	− 0.88
Depth of braincase	−2.755	8.44	−23.42	8.69	−24.11
Interparietal width	−0.572	8.59	− 4.91	8.59	− 4.91
Interparietal length	2.018	4.39	8.86	3.61	7.28
Total mean discriminant score			−5.75		−11.05
Range of discriminant scores		(−6.74 to −4.35)		(−13.75 to −8.81)	

pliers. The range of discriminant scores for the two species was separated by a total score of 4.35.

Liomys irroratus and *Liomys salvini*

These two species are allopatric, their ranges being nearest in Oaxaca, where *irroratus* has been recorded from Zapotitlán and *salvini* from approximately 140 kilometers to the east at Reforma. When a reference sample of *L. irroratus* from the valley of Oaxaca was compared with a reference sample of *L. salvini* from southeastern Oaxaca and northwestern Chiapas, specimens of *irroratus* were found to average larger in all measurements except interparietal width. In the discriminant function analysis, interorbital constriction was weighted (high, positive value) much more than any other measurement (Table 33). Interparietal width and zygomatic breadth had the largest negative discriminant multipliers. The skull of *irroratus* was generally larger than that of *salvini*, with the interorbital constriction of *salvini* being proportionately narrower (20.5 per cent of greatest length of skull in *salvini* as compared with 24.2 per cent in *irroratus*) and the interparietal proportionately wider. The range of discriminant scores for *L. irroratus* and *L. salvini* was separated by more than four points.

Liomys pictus and *Liomys salvini*

These two species are sympatric in southeastern Oaxaca and northwestern Chiapas—from the vicinity of Reforma, Oaxaca, to the vicinity of Tonalá, Chia-

TABLE 33.—*Multipliers and scores resulting from a discriminant function analysis comparing* Liomys salvini *from southeastern Oaxaca and northwestern Chiapas and* Liomys irroratus *from central Oaxaca.*

		L. salvini		*L. irroratus*	
Measurements	Discriminant multiplier	Mean	Mean discriminant score	Mean	Mean discriminant score
Total length	−0.027	207.10	− 5.59	266.89	− 7.21
Length of tail	0.086	100.32	8.63	143.92	12.38
Length of hind foot	0.232	27.03	6.27	32.65	7.57
Greatest length of skull	−0.300	31.37	− 9.41	33.64	−10.09
Zygomatic breadth	−0.533	14.67	− 7.82	15.92	− 8.49
Interorbital constriction	3.143	6.44	20.24	8.14	25.58
Mastoid breadth	0.743	13.80	10.25	15.00	11.15
Length of nasals	−0.198	11.73	− 2.32	13.00	−2.57
Length of rostrum	0.326	13.32	4.34	15.14	4.94
Length of maxillary toothrow	−0.434	4.76	− 2.07	5.38	− 2.33
Depth of braincase	0.452	8.58	3.88	9.12	4.12
Interparietal width	−0.938	8.70	− 8.16	8.50	− 7.97
Interparietal length	−0.721	3.92	− 2.83	3.99	− 2.88
Total mean discriminant score			24.20		15.41
Range of discriminant scores			(12.83-17.00)		(21.05-26.02)

pas. The two species apparently are not ecologically segregated in this area (based upon available field notes). As pointed out earlier, males of *pictus* from the area of sympatry are larger than those from contiguous samples and males of *salvini* are smaller than those in contiguous samples. In order to examine this relationship, a ratio diagram was prepared (Fig. 49) in which the upper diagram is of allopatric populations of the two species that are contiguous with the sympatric populations (sample 24 of *pictus* and sample 2 of *salvini* from the analysis of geographic variation). Specimens of *L. pictus* appear to be proportionally longer in total length and length of tail and have a broader interorbital region. Generally, specimens of *pictus* were larger than those of *salvini*, although in greatest length of skull, zygomatic breadth, mastoid breadth, and interparietal width the two averaged the same or nearly so. The lower ratio diagram (Fig. 49) is of the sympatric populations of males from southeastern Oaxaca and northwestern Chiapas (sample 25 of *pictus* and sample 1 of *salvini* from the analysis of geographic variation). The mean of the measurements have maintained essentially the same proportional relationship to each other, but the values for *pictus* have been shifted to the right, indicating a greater difference between the species in the area of

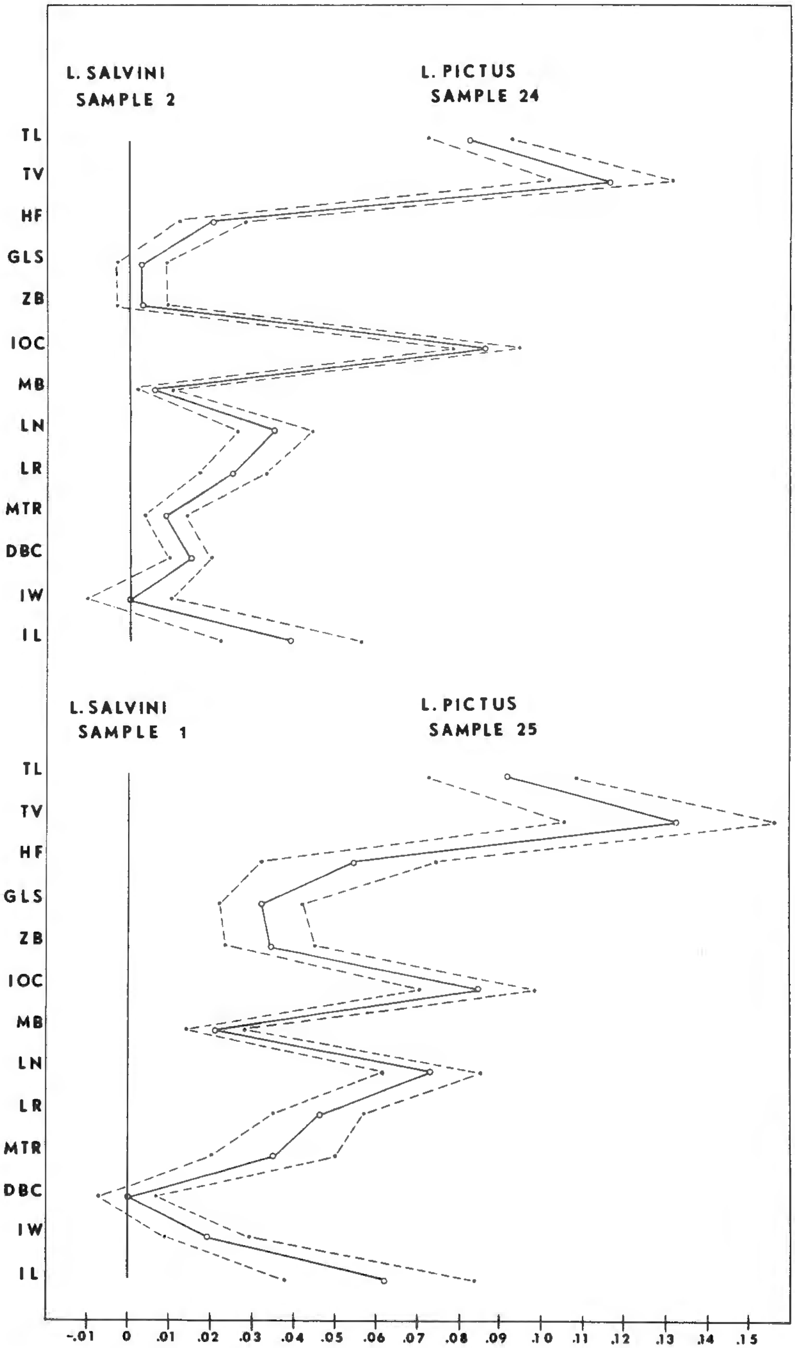


FIG. 49.—Ratio diagrams comparing 13 external and cranial measurements of allopatric samples of *Liomys salvini* and *Liomys pictus* (upper) and sympatric samples of *Liomys salvini* and *Liomys pictus* (lower).

TABLE 34.—*Multipliers and scores resulting from a discriminant function analysis comparing* Liomys pictus *and* Liomys salvini *from southeastern Oaxaca and northwestern Chiapas.*

Measurements	Discriminant multiplier	*L. pictus* Mean	*L. pictus* Mean discriminant score	*L. salvini* Mean	*L. salvini* Mean discriminant score
Total length	−0.001	248.86	− 0.25	206.44	− 0.21
Length of tail	0.084	132.59	11.14	100.39	8.43
Length of hind foot	0.096	29.46	2.83	27.22	2.61
Greatest length of skull	−1.640	32.41	−53.15	31.28	−51.30
Zygomatic breadth	0.954	14.87	14.19	14.62	13.95
Interorbital constriction	1.607	7.82	12.57	6.47	10.40
Mastoid breadth	−0.083	14.03	− 1.16	13.77	− 1.14
Length of nasals	1.807	12.85	23.22	11.59	20.94
Length of rostrum	0.323	14.50	4.68	12.26	3.96
Length of maxillary toothrow	0.565	4.89	2.76	4.74	2.68
Depth of braincase	−2.563	8.73	−22.37	8.61	−22.07
Interparietal width	−0.988	8.72	− 8.62	8.77	− 8.66
Interparietal length	2.087	4.50	9.39	3.93	8.20
Total mean discriminant score			−4.77		−12.21
Range of discriminant scores		(−7.17 to −2.74)		(−13.69 to −10.73)	

sympatry. These results have been interpreted as indicating that males of both *salvini* and *pictus* have undergone character displacement (Brown and Wilson, 1956) in the area of sympatry between the two species.

The most likely explanation for this character displacement is competition between these solitary, rather aggressive mice; it may somehow relate to the breeding biology of these animals, because character displacement is observed only in males and not in females. Whatever the answer is, it will not be known until much more information is available on the biology of these species and until they have been studied more intensively in the area of sympatry.

A discriminant function analysis was performed also on the specimens from the area of sympatry (Table 34). Large positive discriminant multipliers were generated for interorbital constriction, length of nasals, and interparietal length, whereas large negative multipliers were generated for greatest length of skull, depth of braincase, and interparietal length. The range of discriminant scores for *Liomys pictus* was −7.17 to −2.74 and for *Liomys salvini* was −13.69 to −10.73, giving a separation of 3.56.

Liomys pictus and *Liomys spectabilis*

The restricted geographic range of *Liomys spectabilis* (southeastern Jalisco) is completely sympatric with the range of *Liomys pictus plantinarensis*, although

TABLE 35.—*Multipliers and scores resulting from discriminant function analyses comparing* Liomys spectabilis *and* Liomys pictus plantinarensis *from southeastern Jalisco, and* Liomys pictus pictus *from southwestern Jalisco.*

Measurements	Discriminant multiplier	*L. spectabilis* Mean	*L. spectabilis* Mean discriminant score	*L. pictus* Mean	*L. pictus* Mean discriminant score
		Southeastern Jalisco			
Length of hind foot	0.968	30.46	29.49	25.83	25.00
Greatest length of skull	0.758	34.16	25.89	30.09	22.81
Zygomatic breadth	0.479	15.65	7.50	13.97	6.69
Interorbital constriction	1.305	7.98	10.41	7.18	9.37
Mastoid breadth	1.034	14.58	15.08	13.45	13.91
Length of nasals	−1.291	13.63	−17.60	11.53	−14.89
Length of rostrum	0.133	15.52	2.06	12.83	1.71
Length of maxillary toothrow	0.049	5.25	0.26	4.70	0.23
Depth of braincase	−1.785	8.44	−15.07	8.01	−14.30
Interparietal width	−0.127	8.59	− 1.09	8.29	− 1.05
Interparietal length	0.284	4.39	1.25	3.63	1.03
Total mean discriminant score			50.51		58.18
Range of discriminant scores			(56.30-59.82)		(48.49-52.27)
		Southwestern Jalisco			
Length of hind foot	0.205	30.46	6.24	28.65	5.87
Greatest length of skull	0.732	34.16	25.01	31.86	23.32
Zygomatic breadth	−0.677	15.65	−10.60	14.89	−10.08
Interorbital constriction	−2.640	7.98	−21.07	7.67	−20.25
Mastoid breadth	1.134	14.58	16.53	14.21	16.11
Length of nasals	−2.907	13.63	−39.62	12.86	−37.38
Length of rostrum	3.845	15.52	59.67	13.94	53.60
Length of maxillary toothrow	1.069	5.25	5.61	4.92	5.26
Depth of braincase	−1.837	8.44	−15.50	8.33	−15.30
Interparietal width	0.734	8.59	6.31	8.79	6.45
Interparietal length	−0.444	4.39	− 1.95	4.47	− 1.98
Total mean discriminant score			30.63		25.62
Range of discriminant scores			(29.76-32.40)		(23.76-27.42)

the range of *spectabilis* is near the eastern limit of the geographic range of *pictus* at this point. Specimens of *spectabilis* averaged larger than specimens of *L. p. plantinarensis* in all measurements (Table 35). Length of hind foot, greatest length of skull, interorbital constriction, and mastoid breadth all had large positive discriminant multipliers, whereas length of nasals and depth of braincase

TABLE 36.—*Multipliers and scores resulting from a discriminant function analysis comparing* Liomys salvini *from Nicaragua and Costa Rica and* Liomys adspersus *from Panamá.*

Measurements	Discriminant multiplier	*L. salvini* Mean	*L. salvini* Mean discriminant score	*L. adspersus* Mean	*L. adspersus* Mean discriminant score
Total length	−0.017	232.90	− 3.96	257.73	− 4.38
Length of tail	0.035	117.10	4.10	130.60	4.57
Length of hind foot	0.161	27.83	4.48	30.80	4.96
Greatest length of skull	−0.595	32.45	−19.31	35.47	−21.10
Zygomatic breadth	0.001	14.95	0.01	16.59	0.02
Interorbital constriction	1.218	6.83	8.32	7.55	9.20
Mastoid breadth	0.161	13.84	2.23	14.68	2.36
Length of nasals	0.204	12.55	2.56	14.50	2.96
Length of rostrum	1.425	13.91	19.82	15.72	22.40
Length of maxillary toothrow	1.411	4.93	6.96	5.35	8.40
Depth of braincase	1.618	8.45	13.67	9.47	15.32
Interparietal width	−0.158	8.42	−1.33	7.88	− 1.25
Interparietal length	0.362	4.14	1.50	4.56	1.65
Total mean discriminant score			39.05		45.11
Range of discriminant scores			(37.45-40.96)		(42.95-47.24)

had high negative discriminant multipliers. The ranges of discriminant scores for the two taxa were separated by more than four points.

Specimens of *L. spectabilis* also were compared with a sample of *L. p. pictus* from southwestern Jalisco (Table 35). The average values for the *spectabilis* sample were larger for all measurements except interparietal width and interparietal length; also, there was little difference in the average depth of braincase for the two taxa. Greatest length of skull, mastoid breadth, length of maxillary toothrow, and interparietal width had relatively large positive discriminant multipliers, whereas interorbital constriction, length of nasals, and depth of braincase had large negative multipliers. Range of discriminant scores for *L. spectabilis* was 29.76 to 32.40 and for *L. p. pictus* was 23.76 to 27.42.

Liomys salvini and *Liomys adspersus*

These two species are not sympatric, *Liomys adspersus* being isolated in central Panamá and forming the southern limit of distribution of the genus. *Liomys salvini* is known no farther south than central Costa Rica; therefore, the geographic ranges of the two species as presently understood are separated by a hiatus of approximately 300 kilometers. Specimens of *adspersus* averaged larger than those of *salvini* in all measurements except interparietal width (Table 36). Four measurements—interorbital constriction, length of rostrum, length of

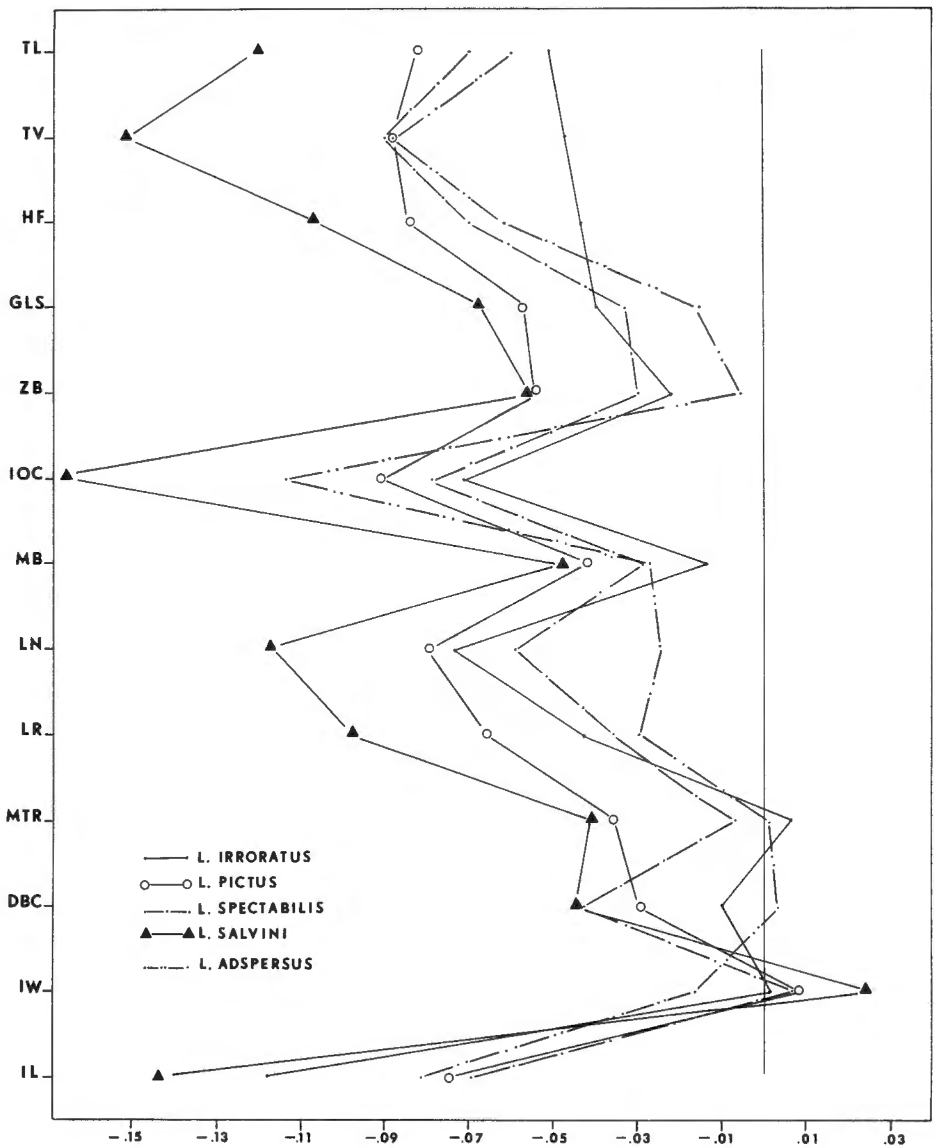


FIG. 50.—Ratio diagram comparing 13 external and cranial measurements of five species of *Liomys* with *Heteromys desmarestianus*. Symbols representing each species of *Liomys* are given at lower left.

maxillary toothrow, depth of braincase—had large positive discriminant multipliers, but only one measurement, greatest length of skull, had a relatively large negative multiplier. The range of discriminant scores for *salvini* was 37.45 to 40.96 and for *adspersus* was 42.95 to 47.24.

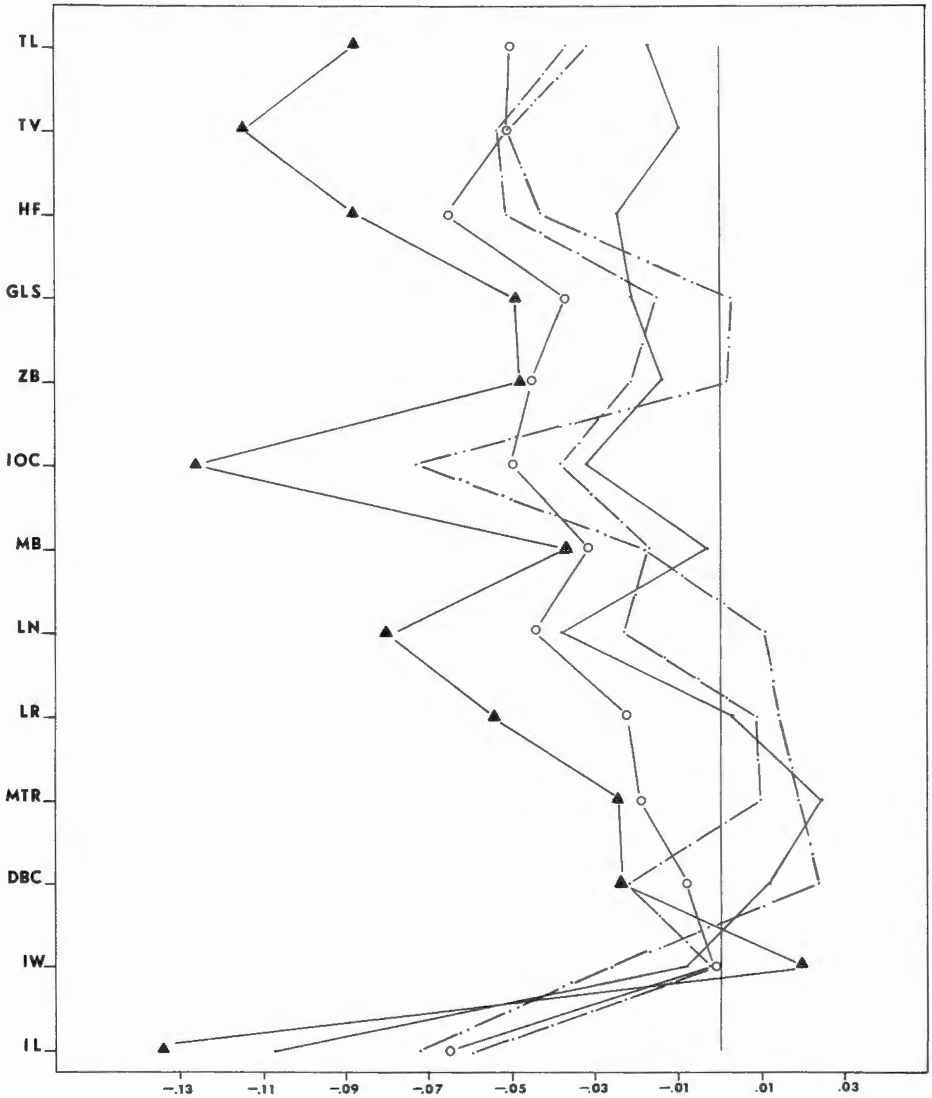


FIG. 51.—Ratio diagram comparing 13 external and cranial measurements of five species of *Liomys* with *Heteromys gaumeri*. Symbols for species of *Liomys* as in Fig. 50.

Heteromys and *Liomys*

Samples of the five species of *Liomys* were compared with *Heteromys desmarestianus* and *Heteromys gaumeri* using ratio diagrams. In nearly all measurements, *Heteromys desmarestianus* was larger than specimens of any species of *Liomys* (Fig. 50). However, interparietal width of four species of *Liomys* (only *adspersus* was less) was greater than in *Heteromys desmarestianus*. Also, *Liomys irroratus* and *L. adspersus* had longer maxillary toothrows and *L. adspersus* had a deeper braincase. Other measurements in which most of the species of *Liomys* converge toward *Heteromys* were greatest length of skull, zygomatic breadth, and mastoid breadth. Measurements of *Liomys* that appear to be most divergent from those of *Heteromys desmarestianus* were interorbital constriction, length of nasals, interparietal length, and length of tail.

Specimens of *Heteromys gaumeri* are generally smaller than those of *H. desmarestianus* and consequently exhibit less size difference when compared with the species of *Liomys*; however, the pattern of variation is similar (Fig. 51). Specimens of *Liomys adspersus* were larger than those of *H. gaumeri* in greatest length of skull, zygomatic breadth, length of nasals, length of rostrum, length of maxillary toothrow, and depth of braincase. Specimens of *Liomys irroratus* were larger than *H. gaumeri* in three measurements (length of rostrum, length of maxillary toothrow, depth of braincase); *L. spectabilis* was larger in two measurements (length of rostrum, length of maxillary toothrow); *L. salvini* was larger in one measurement (interparietal width). Besides length of rostrum and length of maxillary toothrow, other measurements of *Liomys* that converge toward those of *H. gaumeri* are greatest length of skull, zygomatic breadth, mastoid breadth, and interparietal width. Those measurements of *Liomys* that appear to diverge most strongly from *Heteromys gaumeri* were interorbital constriction and interparietal length. Specimens of *Heteromys* (all KU) used in these comparisons are listed below.

Heteromys desmarestianus.—4 mi. S Altamirano, Chiapas, 1; Finca El Paraíso, 4050 ft., Chiapas, 1; 8 mi. NW (by road) Pueblo Nuevo, 5900 ft., Chiapas, 3; Sabana de San Quintin, 215 m., Chiapas, 1; Río Queleya, ½ mi. E Yepocapa, 4300 ft., Chimaltenango, Guatemala, 1; 1 mi. SW Santiago Sacatepéquez, Sacatepéquez, Guatemala, 2; Bonanza, Zelaya, Nicaragua, 1; 2 km. N, 6 km. E Esquipulas, 960 m., Matagalpa, Nicaragua, 2; Hda. Tepeyac, Matagalpa, Nicaragua, 3; 5 mi. S, 2 mi. E Jinotega, Jinotega, Nicaragua, 1; Santa María de Ostuma, 1250 m., Matagalpa, Nicaragua, 2; 5 km. SE Turrialba, Cartago, Costa Rica, 2.

Heteromys gaumeri.—3 km. N Pisté, Yucatán, 3; 6 km. N Tizimín, Yucatán, 1; 1.5 km. S, 1 km. E Pueblo Nuevo X-can, Quintana Roo, 1; 1 km. SSW Santa Rosa, Quintana Roo, 1; 7 km. N, 51 km. E Escárcega, Campeche, 3; 7½ km. W Escárcega, 65 m., Campeche, 1; 103 km. SE Escárcega, Campeche, 1.

Tooth Structure

The unworn upper and lower premolars of *Liomys irroratus*, *L. pictus*, and *L. salvini*, and *Heteromys desmarestianus*, *H. gaumeri*, and *H. lepturus* are here described and compared. The premolars of *L. adspersus* and *L. spectabilis* are not figured and are mentioned only briefly in accounts of other species because adequate material at the proper stage of eruption and wear was not available for study. The structure and wear was not available for study. The structure and wear sequences of the molars of all five Recent species of *Liomys* and the three species of *Heteromys* listed above also are described and compared.

All teeth figured and discussed were in the right toothrow. Dental nomenclature has been modified from Wood (1935:79), Wood and Wilson (1936:388-391), and Shotwell (1967:11). Wood (1935) gave an excellent discussion of the teeth of these two genera.

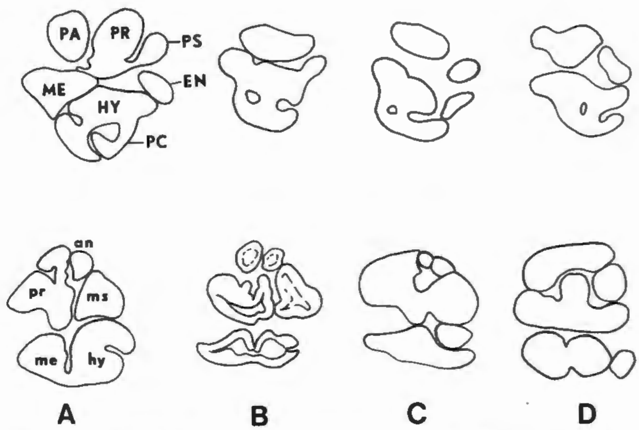


FIG. 52.—Crown patterns of the upper (top) and lower (bottom) premolars of three species of *Liomys* and of *Heteromys* (upper and lower from different species). All teeth illustrated are from the right side. For all teeth, anterior is to the top; for the upper premolar, lingual is to the right and for the lower premolar it is to the left. Abbreviations for the upper premolar are: EN, entostyle; HY, hypocone; ME, metacone; PA, paracone; PC, posterior cingulum; PR, protocone; PS, protostyle. Abbreviations for the lower premolar are: an, anteroconid; hy, hypoconid; me, metaconid; MS, mesoconid; pr, protoconid. The species are as follows: A, *Liomys irroratus* (upper, KU 31174; lower,KU 31129); B, *Liomys pictus* (KU 107667; KU 99792); C, *Liomys salvini* (KU 71118; KU 83963); D, *Heteromys gaumeri* (upper, KU 92146) and *Heteromys desmarestianus* (lower, KU 71255).

Upper Premolar

Liomys irroratus (Fig. 52A).—The protoloph of the upper premolar consists of three cusps arranged more or less in a straight line. The cusps are more distinct in some individuals than others, but are discernable in all specimens examined. The middle cusp, protocone, is the largest of the three and is located directly anterior to the hypocone of the metaloph. The labial cusp, paracone, is smaller than the protocone, but larger than the protostyle. As pointed out by Wood (1935:199), the cusp called the "paracone" may not represent that cone, but rather a labial style.

The metaloph also consists of three cusps, but these are arranged in a crescent with the large middle cusp being the posteriormost. This middle cusp, which represents the hypocone, although largest of the three cusps of the metaloph, is not much larger than the labial metacone. The entostyle, which is noticeably smaller than the metacone and hypocone, is located anterior and slightly lingual to the hypocone.

The entostyle is clearly distinct from the hypocone, but is not as widely separated from it as in *Liomys salvini* and *Heteromys*. The median valley separating the protoloph and metaloph is reminiscent of the Y-shape found in *L. salvini* and *Heteromys*, but the re-entrant angle between the hypocone and entostyle is not continuous with the lingual margin of the tooth. Thus the median valley has a shape of a Y with one arm shorter than the other. As the premolar wears the hypocone and entostyle are quickly united. A well-developed posterior cingulum extends from about the middle of the metacone to the lingual edge of the hypocone. Between this cingulum and the hypocone is a deep pit of enamel, which persists for some time as an island of enamel surrounded by dentine as the tooth is worn.

Liomys pictus (Fig. 52B).—The protoloph of this species appears to consist of a single cusp, which is probably the protocone. In some specimens, there is a slight development of lateral accessory cusps, but these are extremely weak and only occasionally present. Wood (1935:198) stated in his description of the teeth of *Liomys* that the anterior loph of the upper premolar always was composed of three cusps with the central cusp being the largest and "the two lateral ones compressed almost beyond recognition." Certainly these lateral cusps are much more difficult to discern on the premolar of specimens of *pictus* than in *irroratus*.

The metaloph is crescent-shaped and consists of three cusps as in *irroratus*. However, the cusps are all connected by a loph so that they never form discrete cones as in *irroratus*. The hypocone is the largest of the three, but the metacone is almost as large. The smaller entostyle is placed anterior to the hypocone and almost completely lingual to the hypocone. The position of the entostyle is more lingual in *pictus* than in *irroratus* and it is never separated from the other cusps, always being connected by a loph to the hypocone. The median valley separating the protoloph and metaloph has a shape much as in *irroratus*. The re-entrant angle between the entostyle and hypocone does not reach the lingual edge of the tooth so that the median valley is Y-shaped, with one of the arms being shorter than the other.

A well-developed posterior cingulum extends from the middle of the metacone to near the level of the lingual edge of the hypocone. A ridge extends posteriorly from the hypocone and connects with the cingulum, and the lingual end of the cingulum may be connected with the ridge extending from the entostyle to the hypocone or it may be free. However, even in the specimen that is figured, slight wear will connect the cingulum with the ridge extending posteriorly from the entostyle. There is a deep valley of enamel between the posterior cingulum and the hypocone, which is divided in half by the ridge extending posteriorly from the hypocone. These two pits of enamel remain as islands surrounded by dentine as the tooth begins to wear. The valley between the hypocone-metacone-cingulum does not persist as long as the one between hypocone-entostyle-cingulum.

On the two specimens of *Liomys spectabilis* that show the least amount of wear on P4, the pattern of cusps appears to be much as in *L. pictus*, although I am uncertain of exact details.

Liomys salvini (Fig. 52C).—The protoloph of the upper premolar of this species appears to be composed of a single cusp, the protocone, because the two lateral cusps are so compressed against it that they are indistinguishable (Wood, 1935:198). The crescent-shaped metaloph is always composed of at least three cusps and many times four. The metacone is as large, and in some cases larger, than the hypocone. The extra cusp seen on the premolars of many specimens appears to be the result of a deep re-entrant angle of enamel that divides a loph, extending from the hypocone toward the entostyle. This cusp quickly becomes joined with the hypocone as wear to the tooth begins, although the re-entrant angle of enamel is evident for some time (first as an angle of enamel extending from the lingual edge of the tooth into the lake of dentine formed by wear and then as an island of enamel surrounded by dentine). The entostyle is placed anterior and lingual to the hypone and is separated from the other cusps of the metaloph by a re-entrant angle of the median valley. The median valley has a Y-shape much as in *Heteromys*, but as the tooth begins to wear the entostyle does become connected with the hypocone, thus giving the median valley a shape as in the other species of *Liomys*. A well-developed posterior cingulum is present on P4 of *L. salvini*. The cingulum extends from the metacone to the lingual side of the hypocone and is separated from the hypocone by a re-entrant angle of enamel, which eventually forms an island before disappearing.

Although I have not examined extensive material of *Liomys adspersus*, the pattern of the premolars appears to be essentially as it is in *L. salvini*. Certainly the isolated entostyle, which is characteristic of *salvini* and not other species of *Liomys*, is present in *adspersus* as shown by Fleming (1969:82-83, 1971:27).

Heteromys (Fig. 52D).—The description of the premolar for this genus is based mainly on *Heteromys gaumeri* because only specimens of that species were available with unworn premolars. Specimens of *Heteromys desmarestianus* and *Heteromys lepturus* were also examined, but most possessed teeth that were worn to a degree so as to be of only limited use.

The protoloph is composed of three cusps. The centrally located protocone is the largest, but the labially situated "paracone" also is relatively large. The protostyle is small and not evident in some specimens. The metacone and hypocone are located side-by-side on the metaloph, with the entostyle located almost directly anterior to the hypocone. The metacone is the largest cusp and the entostyle is relatively larger than in any of the species of *Liomys*. The median valley that divides the protoloph from the metaloph extends a branch between the hypocone and entostyle, giving the valley a Y-shape. The hypocone and entostyle do become connected at their labial margins, but a portion of the re-entrant angle of enamel persists between the two cusps, in some specimens until they are old adults.

A well-developed posterior cingulum extends from approximately the middle of the metacone to the middle of the hypocone. It is separated from the hypocone by a re-entrant angle of enamel from the lingual side of the tooth. As the tooth begins to wear, this angle becomes an island of enamel surrounded by dentine. This lake may persist for some time, but certainly not so long as the angle between the entostyle and the hypocone.

Lower Premolar

Liomys irroratus (Fig. 52A).—The protolophid of this species is generally composed of three cusps. The two lateral cusps, protoconid (lingual) and mesoconid (labial), are large, but there is variability among individuals as to which is the largest. The anteriorly-placed anteroconid is smaller than the other two cusps and in many instances (as in the specimen figured) this cusp appears to be divided into at least two cusps (see also Wood, 1935:198-199). However, as wear progresses this division is quickly obliterated. The median valley separating the protolophid and metalophid is connected with a deep re-entrant angle that separates the protoconid and mesoconid at their posteriomedial borders. The enamel valley separating the mesoconid and protoconid extends anteriorly between the mesoconid and anteroconid and deeply separates these two cusps. A much shallower branch of this re-entrant angle separates the anteroconid and protoconid. These latter two cusps become joined relatively early in the wear of the tooth, whereas the mesoconid remains separated for a much longer time.

The metalophid is composed of two large cusps, which are situated side-by-side but separated by a shallow angle of enamel. The labial hypoconid is generally larger than the lingual metaconid. These two cusps quickly become united into a single loph as wear progresses.

No anterior cingulum was observed in the specimens of *irroratus*. The only possible remnant of a posterior cingulum is a re-entrant angle of enamel that extends one-third to one-half the way across the hypoconid from its labial side. This angle may persist for a short time as an island of enamel surrounded by dentine as wear progresses.

Liomys pictus (Fig. 52B).—The protolophid of *pictus* is composed of three cusps as in *L. irroratus*. The protoconid is relatively larger than in *irroratus*; it appears to be expanded labially and has nearly filled the space occupied by the re-entrant angle separating the protoconid and mesoconid. In some specimens (as the one figured), the re-entrant angle of enamel extending between the protoconid and mesoconid has been completely blocked by the protoconid, but in other specimens a small valley of enamel temporarily separates the two cusps. The mesoconid is smaller than the protoconid. The anteroconid appears to be composed of two cusps as in *irroratus*; however, as in *irroratus*, these quickly become united. The angle of enamel separating the protoconid from the anteroconid is much deeper and persistent than is the angle between the mesoconid and anteroconid; therefore, contrary to the condition in *irroratus*, the mesoconid and anteroconid first become united as wear progresses and then the anteroconid and protoconid. The mesoconid and protoconid are united early in the wear of the tooth at their posteromedial margins, with a deep pit of enamel, the remnant of the re-entrant angle seen in *irroratus*, forming an island in the middle of the protolophid. I did not observe an anterior cingulum on any specimen of this species.

The metalophid, which is separated from the protolophid by a deep median valley of enamel, is made up of two cusps, hypoconid and metaconid, that quickly become united into a single loph. The lingual metaconid is smaller than the labial hypoconid. A labial re-entrant angle of enamel extends about one-half the distance across the hypoconid. The area posterior to this angle may represent the posterior cingulum. Unfortunately this re-entrant angle is not well developed in the specimen figured, but on other specimens it is as well developed as in the specimen of *irroratus* figured.

Liomys spectabilis appears to have essentially the same cusp pattern as found in *pictus*.

Liomys salvini (Fig. 52C).—The protolophid is composed of three cusps as in the two previous species. However, the cusps are rather weakly defined in *salvini* because the enamel angles separating them are shallow. The mesoconid and protoconid are about equal in size and only slightly separated, if at all, at their posteromedial borders. The anteroconid appears to be composed of two cusps, which are weakly separated from the protoconid and mesoconid. There is a deep pit of enamel near the center of this loph where all of the re-entrant angles coalesce between the cusps. All cusps appear to become united almost simultaneously early in the wear of the tooth leaving an island of enamel near the center of the loph. No anterior cingulum was observed on specimens examined.

The configuration of the metalophid is somewhat different than in *irroratus* and *pictus*. The re-entrant angle of enamel seen in those species extends to, and is united with, the deep median valley of enamel separating protolophid and metalophid; thus, a large cusp (hypoconid) is isolated on the labial margin of the tooth. The area posterior to this angle of enamel is probably a posterior cingulum as supposed for the two earlier species. In none of the specimens that I have examined is a break evident between the metaconid and the posterior cingulum. The separation of the hypoconid remains longer than the separation of cusps of the protolophid, but eventually the hypoconid and metaconid unite to form a single straight loph.

The lower premolars of *Liomys adspersus* exhibit basic features similar to those seen in *L. salvini*.

Heteromys (Fig. 52D).—The lower premolars of mice of this genus are distinct from those of *Liomys*. Instead of being composed of two lophs as in the latter, the lower premolars of *Heteromys* are composed of three or four lophs. The three species that I had available for study had only three lophs on the premolar, but Wood (1935:204-205) described in detail the teeth of some species with four lophs.

The anteriormost loph is formed by a well-developed anterior cingulum. This cingulum may consist of two or more cusps. Behind the anterior cingulum is a loph composed of three cusps, although in none of the specimens that I have examined are these three cusps ever separated from each other. The protoconid and mesoconid are united along their medial margins into a single straight loph. The anteroconid is attached to the anteromedial margin of the loph formed by the protoconid and mesoconid. In the species with four lophs, the anteroconid has been forced out of the protolophid and forms the new loph along with a labial and lingual style left behind by the migrating anterior cingulum (Wood, 1935: 204-205). As the premolars of specimens examined begin to show wear, the anteroconid first is connected with the lingual margin of the anterior cingulum.

The metalophid, which is separated from the protolophid by a deep median valley of enamel, is composed of a hypoconid and metaconid, which are united into a single straight loph. There is a style developing on the labial margin of the tooth; this style does not appear to represent the same development seen on the labial margin of the metalophid of *Liomys* where a re-entrant angle developed in this region. There does not appear to be a posterior cingulum in *Heteromys*.

Specimens used in comparisons of premolars are listed below.

Liomys irroratus.—1 mi. SSE Ameca, Jalisco, 4 (KU 31127-29, 31134); 4 mi. NE Ocotlán, Jalisco, 4 (KU 31156, 31164, 31174, 31185); 2 mi. WNW Ocotlán, Jalisco, 1 (KU 31187); 3 mi. ENE Santa Cruz de las Flores, Jalisco, 1 (KU 31178); 3½ mi. WNW Zapoltitic, Jalisco, 5 (KU 97189, 97196-97, 9720.-01).

Liomys pictus.—2 mi. SSE Autlán, Jalisco, 4 (KU 31205-06, 31214-15); 11 mi. SW Autlán, Jalisco, 3 (KU 107666-68); 2 mi. ESE Tequila, Jalisco, 1 (KU 33459); 7 3/10 mi. ESE Amatlán de Cañas, Nayarit, 1 (KU 100496); 10 mi. S Juchatengo, Oaxaca, 2 (KU 98774, 98780); 20 mi. S, 5 mi. E Sola de Vega, Oaxaca, 1 (KU 99792); 1½ mi. N Badiraguato, Sinaloa, 1 (KU 96668); 2 mi. E Costa Rica, Sinaloa, 1 (KU 100495); 8 km. N Villa Unión, Sinaloa, 1 (KU 96010); Boca del Río, Veracruz, 1 (KU 30044).

Liomys salvini.—Km. 24 on highway S Guatemala City, Guatemala, 1 (KU 83963); 3 km. N, 4 km. W Diriamba, Nicaragua, 4 (KU 110440-41, 110444, 110446); Finca Amayo, Nicaragua, 1 (KU 104708); 5 mi. NW Managua, Nicaragua, 1 (KU 71118); 4 mi. W Managua, Nicaragua, 1 (KU 71133); 3 mi. SW Managua, Nicaragua, 3 (KU 71204, 71210, 71212); 3 mi. S Managua, Nicaragua, 1 (KU 71188); 2 km. N Mérida, Nicaragua, 2 (KU 115400-01); 2 km. N, 3 km. E Mérida, Nicaragua, 2 (KU 115403-04); Moyogalpa, Nicaragua, 2 (KU 97933, 115386).

Heteromys desmarestianus.—Río Queleya, ½ mi. E Yepocapa, Guatemala, 1 (KU 65069); 1 mi. SW Santiago Sacatepéquez, Guatemala, 2 (KU 71254-55); 2 mi. SW Santiago Sacatepéquez, Guatemala, 2 (KU 71247, 71252); Sabana de San Quintín, Chiapas, 1 (KU 102653); Hda. Tepeyac, Nicaragua, 1 (KU 104596).

Heteromys gaumeri.—5 km. S Champotón, Campeche, 2 (KU 92146-47); 7 km. W Escárcega, Campeche, 1 (KU 92150); Esmeralda, Quintana Roo, 1 (KU 35196).

Heteromys lepturus.—Vista Hermosa, Oaxaca, 3 (KU 99845, 99849, 99852).

Molars

Liomys (Fig. 53A).—The structure of the upper and lower molars is essentially the same in all species of *Liomys*. All molars are composed of two lophs (protoloph or metalophid and metaloph or hypolophid) separated by a median valley of enamel. The three cusps composing each of the lophs are discernable for only a short period after the tooth has erupted. As pointed out by Wood (1935: 199), Goldman's (1911:32) statement that in members of this genus "loops of molar crowns normally without additional enamel islands even in young" is incorrect. These islands, resulting from the presence of a posterior cingulum dorsally and an anterior cingulum below, are present in the youngest individuals of this genus available, especially on the lower molars, although for a short period of time.

As the molars wear, the protoloph and metaloph usually are united at their lingual edge and then at the labial edge. The uniting of these lophs usually does not occur until the permanent premolar is in place. One difference among species of *Liomys* involves the wear pattern of the first upper molar. In *irroratus, pictus,* and most likely *spectabilis,* the protoloph and metaloph meet as described above and as a result an island of enamel representing the middle of the median valley is isolated near the center of the tooth. This island is present in almost all, if not all, individuals of these species at the proper stage of wear and probably persists for some time. In *salvini* and probably *adspersus,* on the other hand, an island of enamel isolated on the first upper molar is a rare occurrence, although I have seen some specimens with this structure (as did Wood, 1935:199). Either this structure

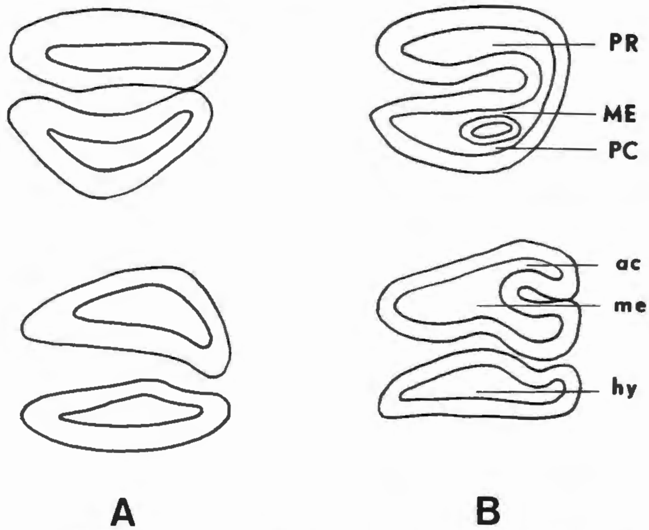


FIG. 53.—Crown patterns of the first upper (top) and lower (bottom) molars of one species of *Liomys* and *Heteromys*. All teeth illustrated are from the right side. For all teeth, anterior is to the top; for the upper molar, lingual is to the right and for the lower is to the left. Abbreviations used in the illustration are: ME, metaloph; PC, posterior cingulum; PR, protoloph; ac, anterior cingulum; hy, hypolophid; me, metalophid. The species are: A, *Liomys irroratus* (KU 97189); B, *Heteromys lepturus* (KU 99845).

is formed only in a few individuals or else the island is present for only a short period of time. The explanation for this difference I believe, is that in *irroratus* and *pictus* the enamel in the median valley is deepest at the center and shallower on the edges (shallowest on lingual margin), whereas in *salvini* the enamel at the center of the tooth is nearly the same depth as on the labial margin of the tooth (again being shallowest at lingual margin).

On the lower molars, the metalophid and hypolophid are first united at their labial edge and later at the lingual edge.

Heteromys (Fig. 53B).—The upper and lower molars of the species of *Heteromys* appear to be composed of three lophs instead of two as seen in all but the youngest specimens of *Liomys*. A well-developed posterior cingulum is present on the upper molars and a well-developed anterior cingulum on the lower molars. In the three species (*desmarestianus*, *gaumeri*, and *lepturus*) that I studied, the posterior cingulum is well developed and is nearly as long as the metaloph. The cingulum is always connected with the metaloph at their lingual margins and free at early stages of wear at the labial margin (this is clearly evident in a specimen of *desmarestianus*, KU 71258, from near Jinotega, Nicaragua). As wear progresses, the labial margins of the cingulum and metaloph are united, thus isolating the enamel valley between them. This island of enamel is present for varying lengths of time; in *gaumeri* the island disappears much more quickly than in *desmarestianus*.

The anterior cingulum on the lower molars were only one-half or less the length of the metalophid. The labial margins of the two lophs are separate before wear begins; as wear progresses, the metalophid and cingulum are united at their labial margin isolating one or more islands of enamel in the metalophid.

The protoloph and metaloph become united at their lingual margins when the deciduous premolar is still present, but the labial margins do not unite until the tooth exhibits considerable wear. I have the impression that the lingual margins of the protoloph and metaloph become united much sooner in *Heteromys* than in *Liomys*, whereas the labial margins of these are united sooner in *Liomys* than in *Heteromys*. In the lower molars, the reverse pattern is seen, with the labial margins of the metalophid and hypolophid being the first to be united and then the lingual margins. Specimens examined in addition to those listed for premolars are as follows.

Liomys salvini.—3 mi. SW Managua, Nicaragua, 3 (KU 71166, 71196, 71215); 2 mi. N Sabana Grande, Nicaragua, 1 (KU 71128). *Heteromys desmarestianus.*—5 mi. S, 2 mi. E Jinotega, Nicaragua, 1 (KU 71258). *Heteromys gaumeri.*—4 km. NNE Felipe Carrillo Puerto, Quintana Roo, 1 (KU 92140); Peto, Yucatán, 1 (KU 93640).

Size of Teeth

Length and width of the upper premolar and first upper molar was measured on selected specimens of all species of *Liomys* and *Heteromys desmarestianus* using a binocular microscope with an ocular micrometer.

On the average, specimens of *Liomys salvini* have the shortest and narrowest premolars of species studied (see Table 37). Specimens of *Liomys irroratus* had on the average the longest and widest upper premolars. When the size of the premolars is considered relative to the overall size of the animal (greatest length of skull used as a standard), specimens of *Heteromys* were found to have much shorter and narrower premolars than specimens of *Liomys*. Essentially these data mean that the premolars of *Heteromys* are actually about the same size as those of *Liomys*, but relative to the overall size of the animals they are smaller.

The first upper molar is shortest in specimens of *Liomys pictus* and *Liomys salvini* and longest in *Heteromys desmarestianus*. This tooth is widest in *Liomys irroratus* and narrowest in *Liomys salvini*. Again, when the size of the tooth is compared to the overall size of the specimen, the length of the first upper molar is somewhat shorter and much narrower in *Heteromys* than in the species of *Liomys*. Specimens used for study of tooth size are listed below.

Liomys irroratus.—Omilteme, Guerrero, 1 (KU 98761); 2 mi. E Omilteme, Guerrero, 1 (KU 98763); 3 mi. NNW Ameca, Jalisco, 3 (KU 39903-05); Cerro la Caldera, México, 1 (KU 28050); 5 mi. S, 1 mi. W Texcoco, México, 1 (KU 49015); Iturbide, Nuevo León, 2 (KU 55950-51); 3 mi. ESE Oaxaca, Oaxaca, 1 (KU 61602); 4 mi. ESE Oaxaca, Oaxaca, 1 (KU 62633); 1 mi. SSW Tilapa, Puebla, 3 (KU 62617-18, 62620); 8 mi. SW Ramos, San Luis Potosí, 2 (KU 59533, 59536); 7 km. S, 2 km. W San Fernando, Tamaulipas, 3 (KU 36949-50, 36952); Río Nieves, 1 mi. N Rancho Grande, Zacatecas, 1 (KU 84697).

Liomys pictus.—Finca San Salvador, 15 km. SE San Clemente, Chiapas, 2 (KU 102647, 102650); 3 3/10 mi. NE Contla, Jalisco, 1 (KU 96040); 2 2/10 mi. NE Contla, Jalisco, 3 (KU 96046-47, 96056); 14 km. S Durazno, Jalisco, 4 (KU 87427-28, 87430-31); 10 mi. S Juchatengo, Oaxaca, 1 (KU 98775); 20 mi. S, 5 mi. E Sola de Vega, Oaxaca, 2 (KU 98768-69); 5 mi. NW Mazatlán, Sinaloa, 4 (KU 85788, 85794-95, 85797); 3 mi. NNW Mazatlán, Sinaloa, 1 (KU 39820); 3 km. E San Andrés Tuxtla, Veracruz, 2 (KU 24026, 24028).

TABLE 37.—*Measurements of the upper premolar and first upper molar of five species of* Liomys *and of* Heteromys desmarestianus.

Statistics	*Liomys irroratus* N=20	*Liomys pictus* N=20	*Liomys spectabilis* N=10	*Liomys salvini* N=20	*Liomys adspersus* N=5	*Heteromys desmarestianus* N=10
			Length P4			
Mean	1.62	1.47	1.59	1.45	1.54	1.55
Minimum	1.45	1.35	1.45	1.30	1.40	1.40
Maximum	2.00	1.70	1.75	1.75	1.70	1.75
1 SE	± 0.031	± 0.024	± 0.035	± 0.025	± 0.051	± 0.036
			Length P4/Greatest length of skull × 100			
Mean	4.88	4.64	4.69	4.59	4.38	4.06
Minimum	4.58	3.94	4.26	4.14	4.00	3.69
Maximum	5.48	5.12	5.13	5.30	4.78	4.62
1 SE	± 0.057	± 0.067	± 0.085	± 0.076	± 0.157	± 0.103
			Length M1			
Mean	1.00	0.93	1.01	0.93	0.99	1.06
Minimum	0.90	0.80	0.90	0.85	0.95	1.00
Maximum	1.15	1.10	1.10	1.10	1.00	1.10
1 SE	± 0.013	± 0.018	±00.019	± 0.013	± 0.010	± 0.014
			Length M1/Greatest length of skull × 100			
Mean	3.02	2.93	2.98	2.96	2.82	2.78
Minimum	2.80	2.45	2.59	2.51	2.67	2.56
Maximum	3.30	3.21	3.26	3.44	2.95	2.93
1 SE	± 0.037	± 0.046	± 0.056	± 0.049	± 0.046	± 0.048

TABLE 37.—*Continued.*

			Width P4			
Mean	1.75	1.55	1.74	1.51	1.65	1.53
Minimum	1.50	1.45	1.55	1.30	1.50	1.35
Maximum	2.10	1.70	1.90	1.60	1.95	1.70
1 SE	± 0.035	± 0.014	± 0.039	± 0.015	± 0.077	± 0.029
			Width P4/Greatest length of skull × 100			
Mean	5.28	4.91	5.13	4.77	4.68	4.01
Minimum	4.79	4.52	4.75	4.41	4.41	3.51
Maximum	5.76	5.38	5.72	5.11	4.72	4.52
1 SE	± 0.063	± 0.061	± 0.122	± 0.049	± 0.140	± 0.084
			Width M1			
Mean	1.72	1.52	1.74	1.42	1.55	1.47
Minimum	1.50	1.25	1.60	1.30	1.50	1.25
Maximum	2.00	1.75	1.85	1.55	1.70	1.60
1 SE	± 0.030	± 0.024	± 0.026	± 0.016	± 0.039	± 0.030
			Width M1/Greatest length of skull × 100			
Mean	5.19	4.80	5.13	4.48	4.40	3.86
Minimum	4.64	3.83	4.75	3.99	4.21	3.21
Maximum	5.76	5.40	5.57	4.84	4.53	4.26
1 SE	± 0.067	± 0.086	± 0.079	± 0.056	± 0.052	± 0.100

Liomys spectabilis.—3 3/10 mi. NE Contla, Jalisco, 4 (KU 96042-45); 3 mi. NE Contla, Jalisco, 1 (KU 96039); 2 2/10 mi. NE Contla, Jalisco, 4 (KU 96049, 96052, 96054, 96064); 8½ mi. S Mazamitla, Jalisco, 1 (KU 97183).

Liomys salvini.—7 mi. SW Filadelfia, Costa Rica, 1 (KU 60480); Monte Rey, 22 km. S San José, Costa Rica, 1 (KU 60657); 1 mi. NW San Salvador, El Salvador, 3 (KU 71074-75, 71079); 5 mi. S Guatemala City, Guatemala, 2 (KU 65030-31); km. 24 on highway S Guatemala City, Guatemala, 3 (KU 83967-69); 1 mi. SE Puerto Madero, Chiapas, 1 (KU 68849); 6 mi. NNW Tonalá, Chiapas, 5 (KU 68839-43); 1 km. NE Esquipulas, Nicaragua, 1 (KU 115363); Hda. Bellavista, Nicaragua, 3 (KU 106379, 106384-85).

Liomys adspersus.—2 km. NE Buenos Aires, Panamá, 5 (KU 121527, 121530, 121532-34).

Heteromys desmarestianus.—2 mi. S Santiago Sacatepéquez, Guatemala, 1 (KU 71250); 8 mi. N Pueblo Nuevo, Chiapas, 1 (KU 84146); 8 mi. (by road) NW Pueblo Nuevo, Chiapas, 3 (KU 95034-36); 7.5 mi. (by road) NW Pueblo Nuevo, Chiapas, 3 (KU 95039, 96813-14); 6 mi. S Pueblo Nuevo, Chiapas, 1 (KU 83974); 5 mi. S, 2 mi. E Jinotega, Nicaragua, 1 (KU 71257).

Morphology of Glans Penis

The value of the glans penis in systematic studies of rodents has been discussed by several recent authors (Hooper, 1958, 1959, 1960, 1961, 1962; Hooper and Hart, 1962; Hooper and Musser, 1964; Hershkovitz, 1966). Most of these papers deal with cricetid rodents, the one exception being a paper on caviomorph rodents (Hooper, 1961); I have been unable to locate any reports on the glandes of heteromyid rodents. Although there were some morphological differences in the glandes of the six species studied, this structure did not exhibit the striking morphological diversity seen in certain other characters, such as the baculum.

Glandes used in this study except that of *Heteromys lepturus* were collected from freshly killed animals and were preserved immediately in 10 per cent formalin. The glans of *lepturus* was removed from a museum study skin and was rehydrated for study. Glandes were placed in a 2 per cent solution of potassium hydroxide until the baculum was faintly visible when examined in strong light. The glandes then were stained with Alizarine Red S. Finally, they were passed through three solutions of glycerine of increasing strength and stored in 100 per cent glycerine (see Hooper, 1958:6).

Final drawings were prepared from camera lucida sketches; glandes were measured using a binocular microscope fitted with an ocular micrometer. Measurements were taken following Hooper (1958:6-7). The protractile tip (Hooper, 1958:6-7), present in all species, was measured in dorsal view. This tip has been termed the bacular mound by some authors (Hooper and Hart, 1962:9; Hooper and Musser, 1964:7, among others); in the present paper I have simply termed this structure as the "tip," but most other terminology follows Hooper (1958:6, 1960:3). The urethral lappets alluded to in the following accounts are paired structures located in the terminal crater, lateral to the urethral opening and ventral to the baculum. Although the urethral lappets are either trilobed or bilobed, in normal position they are folded so as to appear a solid, unlobed structure.

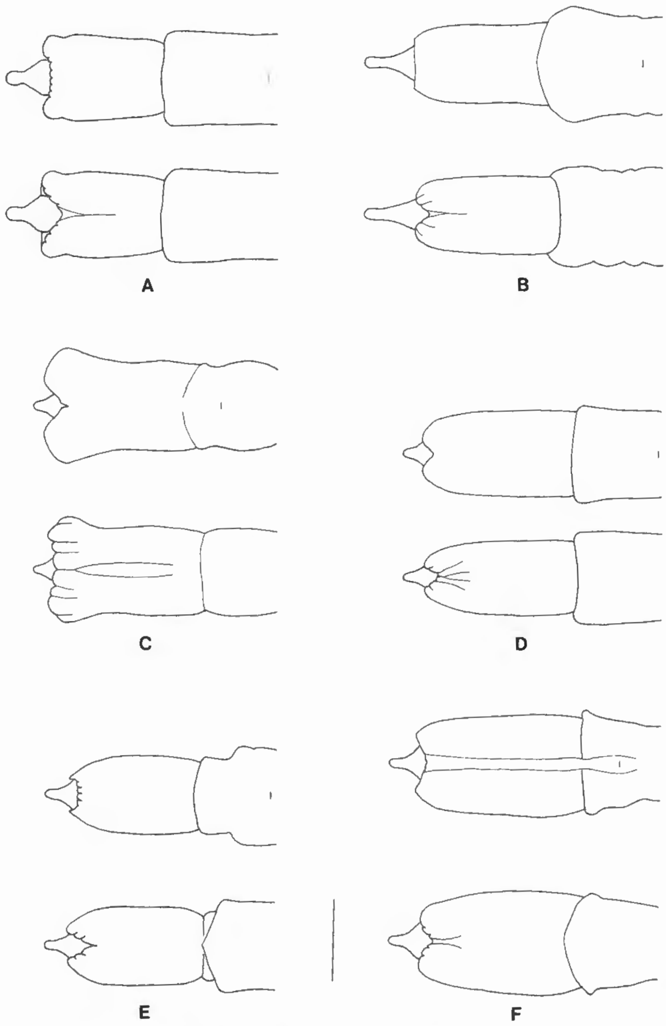


FIG. 54.—Glans penes of five species of *Liomys* and one of *Heteromys*. The upper view in each pair is a dorsal view of the glans and the lower is a ventral view. A small vertical line in dorsal views marks the posterior end of the baculum. Species are as follows: A, *Liomys pictus* (KU 120590); B, *Liomys spectabilis* (KU 120606); C, *Liomys salvini* (KU 120600); D, *Liomys adspersus* (KU 121528); E, *Liomys irroratus* (KU 67721); F, *Heteromys lepturus* (KU 99855). The scale is three millimeters long.

Liomys irroratus (Figs. 54E, 55E).—The glans of *Liomys irroratus* is nonspinous (as in all other species examined), cylindrical, and relatively long compared with the length of the baculum (78.5 per cent the length of the baculum in the one specimen examined—Table 38). The sides of the glans are nearly straight, the widest point being approximately at the mid-point of the glans. A large tip protrudes slightly from, and nearly fills, the terminal crater; the baculum extends to the end of the tip, with no cartilaginous elements present. The diameter of the

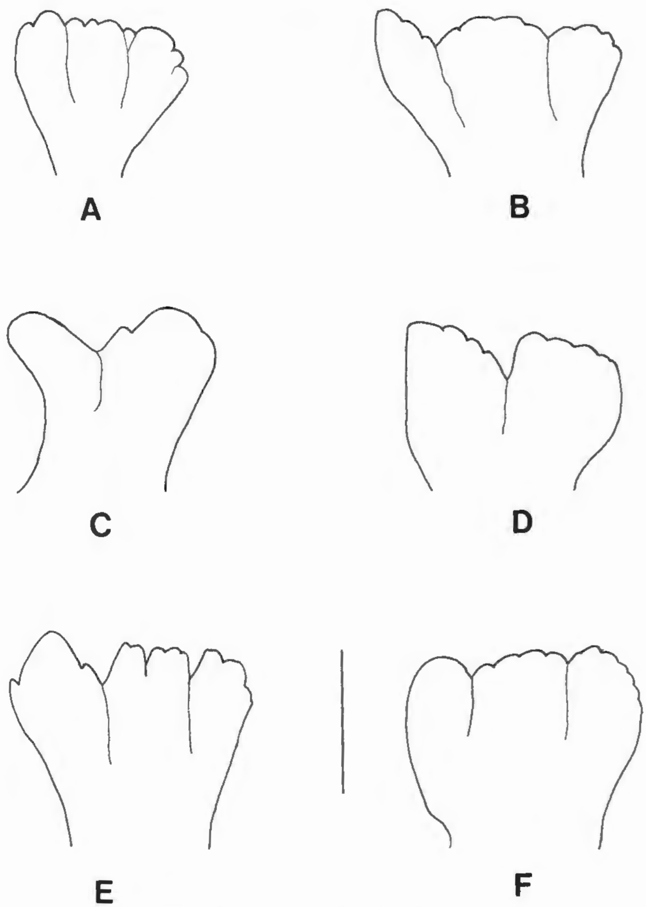


FIG. 55.—Ventral view of the left urethral lappet of five species of *Liomys* and one of *Heteromys*. The species are A, *Liomys pictus* (KU 120590); B, *Liomys spectabilis* (KU 120606); C, *Liomys salvini* (KU 120600); D, *Liomys adspersus* (KU 121528); E, *Liomys irroratus* (KU 67721); F, *Heteromys lepturus* (KU 99855). The scale is one millimeter long. Medial is to the left on the drawing.

glans of *Liomys irroratus* is relatively narrow compared with the length (Table 38). Only one specimen of *Liomys adspersus* (KU 121528) had a glans in which the ratio of the diameter to length was less than in the specimen of *Liomys irroratus.* The rim of the terminal crater is crenulate dorsally and ventrally; the lips are formed into a deep V-shape ventrally so that more of the tip is revealed ventrally than dorsally. The sculpturing on the glans is relatively weak so that the structure appeared relatively simple and featureless. Located in the terminal crater ventral to the baculum was a pair of urethral lappets, which are relatively large and trilobed.

Liomys pictus (Figs. 54A, 55A).—The glans of this species was found to be cylindrical in the basal two-thirds, but somewhat flared at the rim of the terminal crater, which is the broadest portion of the glans. The flaring of the glans in this area may be partly due to swelling during preparation, however, some flaring was evident in all four of the specimens of this species studied. The glans of *pictus* is relatively short compared with the length of the baculum; only one specimen of *Liomys spectabilis* and one specimen of *Liomys adspersus* had glans that were as relatively short as those of *pictus*. The ratio of the diameter of the glans to the length of the glans is highly variable in this species, possibly indicating a swelling of the diameter of some specimens during preparation. The tip protruding from the terminal crater is actually longer (Table 38) in *pictus* than in other species examined except *Liomys spectabilis*; the length of the tip in proportion to the overall length of the glans is similar in *pictus* and *spectabilis*, but much longer in these two species than the other four studied. The rim of the terminal crater is slightly concave dorsally and deeply incised into a deep V ventrally. The rim is crenulated both dorsally and ventrally with the incisions being slightly deeper than in *Liomys irroratus*.

The urethral lappets are located as they were in *L. irroratus* and are trilobed. Of the four species with trilobed urethral lappets, these lappets are smallest in *pictus*.

Liomys spectabilis (Figs. 54B, 55B).—The glans of the single specimen examined of this species is cylindrical in outline, with the broadest portion near the base. The glans of this specimen is longer than all other specimens of *Liomys* studied except one specimen of *L. adspersus;* however, when compared with the length of the baculum, the glans of *spectabilis* is proportionally shorter than in other species studied except *L. pictus* (Table 38). The ratio of the diameter to the length was low for *L. spectabilis*, comparing favorably with values for *L. irroratus* and *L. adspersus*. The tip extended farther beyond the main body of the glans in this species than any other, but in proportion to the total length of the glans, the length of the tip in *spectabilis* was similar to *L. pictus*. The rim of the terminal crater is nearly straight dorsally, but forms a V ventrally, thus exposing more of the tip ventrally than dorsally. The rim displays fairly deeply incised crenulation ventrally, but not dorsally. The urethral lappets of *L. spectabilis* are trilobed. These structures are larger in *spectabilis* than in *pictus*.

Liomys salvini (Figs. 54C, 55C).—The glandes of the two specimens of *Liomys salvini* examined are cylindrical in the basal two-thirds and flared outward in the distal third, being broadest in this region, although I suspect that most of this terminal flaring can be attributed to swelling during preparation. In actual length the glans of this species is the shortest of those species studied; however, compared with the length of the baculum, the glans of *L. salvini* is proportionally longer than the glans of *pictus*, *spectabilis*, and *adspersus*, but shorter than in *irroratus* and *Heteromys lepturus* (Table 38). The diameter of the glans was large compared with the length, possible resulting from swelling of the diameter in preparation. The tip protrudes only a short distance beyond the rim of the terminal crater. The baculum extends to the end of the tip and no cartilaginous structures are present (as in all other species studied). Dorsally, the rim of the terminal crater is notched into a fairly deep V-shape, whereas below no such notch was evident, although this may have been partly due to swelling in this area. In any event, more of the tip is evident dorsally in this species than ventrally. The rim of the crater is crenate ventrally, with the incisions being deeper than in any other species studied save *L. adspersus*. The urethral lappets, in contrast to those of the previous three species, are bilobed. The size of the lappets was medium for those studied.

Liomys adspersus (Figs. 54D, 55D).—The glans of *Liomys adspersus* is cylindrical, being broadest near the mid-point. The ratio of the length of glans to the length of the baculum is less for *adspersus* than for *salvini* and *irroratus* and more for *adspersus* than for *spectabilis* and most specimens of *pictus* (Table 38). The diameter is small compared with the length. The tip extends only a short distance beyond the main body of the glans. Both dorsally and ventrally, the rim of the terminal crater forms a broadly rounded V, thus exposing approximately the same amount of the tip in both views. The rim is relatively smooth above and deeply crenate below. The urethral lappets, as in *Liomys salvini*, are bilobed. The medial lobe of the lappet is larger than the medial lobe in specimens of *salvini*.

Heteromys lepturus (Fig. 54F, 55F).—The glans of the one specimen of *Heteromys lepturus* examined was cylindrical in shape, the broadest point being about one-third of the distance from the base to the tip. The ratio of the length of the glans to the length of the baculum is larger for this species than for the five species of *Liomys* examined, although the one specimen examined of *L. irroratus* closely approaches the value (Table 38). The diameter of the glans is relatively narrow compared with the length. The tip protruded 1.35 beyond the main body of the glans, which, when compared with the length of the glans, was proportionally about the same as for *irroratus*, *salvini*, and *adspersus*. The rim of the terminal crater is concave above and forms a broadly rounded V below. The rim is weakly crenulated dorsally and slightly more so ventrally. The urethral lappets are trilobed as in *irroratus*, *pictus*, and *spectabilis*.

Conclusions.—The glandes of the six species examined exhibit many common characteristics, the differences observed being in many instances in size or degree of development of similar features. All of the glandes are more or less cylindrical in shape, with a protractile tip protruding beyond the rim of the terminal crater. In the tip, the baculum extends to the end and no cartilaginous structures are present. All glandes examined appeared to be nonspinous.

Among these rather homogeneous structures, I believe three morphological types can be distinguished. The first type, represented by *Liomys irroratus* and *Heteromys lepturus*, is characterized by a relatively long glans (compared with the length of baculum), short tip, weak crenulation on the rim of the terminal crater, and trilobed urethral lappets. A second group, composed of *Liomys pictus* and *Liomys spectabilis*, is characterized by possession of a short glans compared with the length of baculum, long tip, slightly stronger crenulation on the rim of the terminal crater than in the first group, and trilobed urethral lappets. The last group, consisting of *Liomys salvini* and *Liomys adspersus*, has a medium-sized glans compared with the length of the baculum, short tip, deeply crenulated rim

TABLE 38.—*Measurements of the glans penes and associated structures of five species of* Liomys *and one of* Heteromys.

Locality and number	Length of distal tract	Length of glans	Length of baculum	Length of glans/ Length of baculum × 100	Diameter of glans	Diameter of glans/ Length of glans × 100	Length of tip
			Liomys irroratus				
Puebla (KU 67721)	8.1	5.5	7.0	78.5	2.85	51.8	1.10
			Liomys pictus				
Jalisco (KU 120590)	9.1	5.4	8.0	67.5	3.30	61.1	1.35
Jalisco (KU 120592)	9.7	5.5	8.5	64.7	4.00	72.7	1.55
Jalisco (KU 120594)	10.6	5.3	8.3	63.4	3.20	60.3	1.50
Jalisco (KU 120587)	9.4	5.6	8.5	65.8	3.00	53.5	1.75
			Liomys spectabilis				
Jalisco (KU 120606)	11.0	6.3	9.8	64.2	3.40	53.9	1.80
			Liomys salvini				
Chiapas (KU 120597)	8.6	5.1	7.0	72.8	3.50	68.6	0.55
Chiapas (KU 120600)	9.2	5.2	7.0	74.2	4.05	77.8	0.90
			Liomys adspersus				
Panamá (KU 121527)	9.3	6.4	9.2	69.5	3.35	52.3	1.25
Panamá (KU 121528)	10.1	5.8	8.7	66.6	3.00	51.7	1.00
			Heteromys lepturus				
Oaxaca (KU 99855)	12.1	6.8	8.6	79.0	3.85	56.6	1.35

on the terminal crater ventrally, and bilobed urethral lappets. Specimens used for study of the glans penis are listed below.

Liomys irroratus.—6.5 mi. SW Izúcar de Matamoros, Puebla, 1 (KU 67721). *Liomys pictus.*—4 km. NE Contla, Jalisco, 1 (KU 120590); 2 km. NW Emiliano Zapata, Jalisco, 1 (KU 120587); 4 km. W Tuxpan, Jalisco, 2 (KU 120592, 120594). *Liomys spectabilis.*—6 km. NE Contla, Jalisco, 1 (KU 120606). *Liomys salvini.*—16 km. SW Tapachula, Chiapas, 2 (KU 120597, 120600). *Liomys adspersus.*—2 km. NE Buenos Aires, Panamá, 2 (KU 121527-28). *Heteromys lepturus.*—3½ mi. SSW Vista Hermosa, Oaxaca, 1 (KU 99855).

Bacular Morphology

Although the existence of a baculum in many mammals had been known since the late 1700's this structure was not studied systematically in North American mammals until the late 1930's and early 1940's in such works as those of Burt (1936) on *Perognathus* and *Dipodomys*, Wade and Gilbert (1940) on squirrels, Burt and Barkalow (1942) on woodrats, and Hamilton (1946) on microtines. Much of this work was summarized in Burt's (1960) compendium, "Bacula of North American mammals." In this treatise, Burt (1960:44) described the bacula of three species of *Liomys* (*irroratus*, *pictus*, and *salvini* under the name *crispus*) and figured the structure of two (*irroratus* and *pictus*). In the following accounts, I have described and figured the bacula of the five recognized species of *Liomys* as well as the bacula of specimens of *Heteromys desmarestianus* and *Heteromys gaumeri*.

Dried penes were removed from museum study skins and soaked in two per cent solution of KOH. The fleshy glans were removed and the cleaned bacula stored in glycerine. Bacula were measured with an ocular micrometer and drawn with the aid of an ocular grid. Bacula are shown in Fig. 56 and measurements of the bacula are given in Table 39.

Liomys irroratus (Fig. 56E).—The baculum of this species is of medium length for the genus. However, compared with overall body size (hind foot used as a standard—see Hooper, 1958:8) the baculum is proportionately the shortest of any species of *Liomys*, but is not so short as that of the two species of *Heteromys* studied. The base of the baculum of *irroratus* is higher than wide as in all species studied. Both the width and height of the base of the baculum of *irroratus* averaged greater than in any other species studied (Table 39).

Bacular morphology of *L. irroratus* bears a striking resemblance to that in the two species of *Heteromys* examined. From the broad, high base, the shaft tapers rapidly for about the first one-third of its length, then gradually to the tip. The shaft is essentially oval in shape to its tip; this feature serves to distinguish *L. irroratus* from other species of *Liomys* and to ally it with *Heteromys*. The tip of the baculum is slightly upturned and simple in construction, although the extreme distal end may be laterally compressed. The extent of this flattened area is individually variable, but never was found to be extensive.

Liomys pictus (Fig. 56A).—In comparison to body size, the baculum of this species and *L. spectabilis* were the longest studied. However, the base is pro-

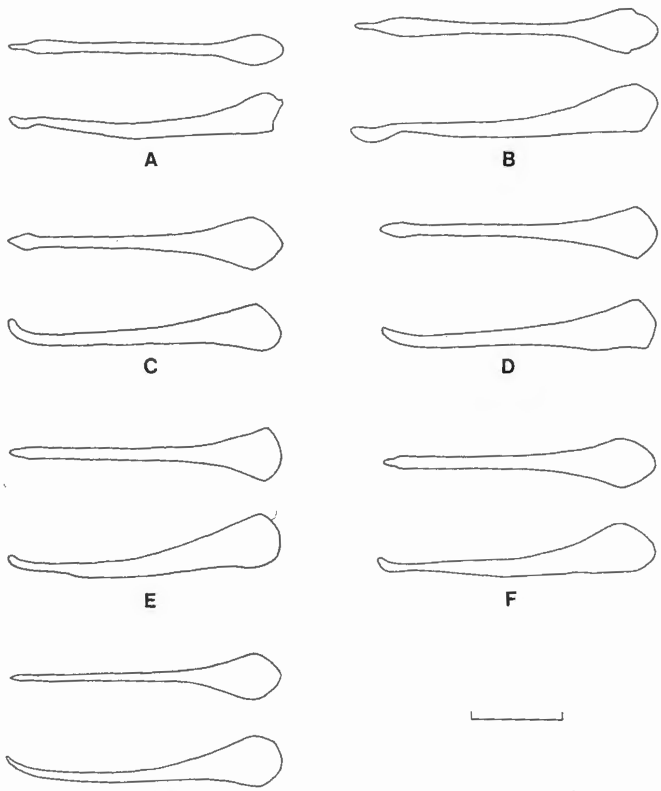


FIG. 56.—Bacula of five species of *Liomys* and two of *Heteromys*. The upper view in each pair is a dorsal view and the lower is a lateral view. The species are as follows: A, *Liomys pictus* (KU 96063); B, *Liomys spectabilis* (KU 96044); C, *Liomys salvini* (KU 71164); D, *Liomys adspersus* (KU 121532); E, *Liomys irroratus* (KU 103781); F, *Heteromys desmarestianus* (KU 71257); G, *Heteromys gaumeri* (KU 92136). The scale at the lower right is three millimeters long.

portionally narrower than in other species of *Liomys*. The base occupies about one-fourth of the total length of the bone. The shaft tapers rapidly from the base and usually is slightly bowed in lateral view. The shaft has a ventrally expanded and laterally compressed keel at its tip, which is from 0.85 to 1.25 millimeters long. Just posterior to the keel, the baculum is dorsoventrally flattened and in dorsal view the shaft appears laterally expanded in this region.

Liomys spectabilis (Fig. 56B).—The baculum of this species is nearly identical morphologically to that of *Liomys pictus*. The only possible difference observed was that the ventral keel at the tip of the shaft is slightly longer in *spectabilis* (1.30 millimeters in the two available bacula).

Liomys salvini (Fig. 56C).—The average length of the baculum of this species is the shortest of any species of *Liomys*, although compared with overall body size, it is in the middle of the range of variation within the genus. The average

TABLE 39.—*Bacular measurements for five species of* Liomys *and two species of* Heteromys.

Statistics	Length of baculum	Length of baculum/ Length of hind foot × 100	Height of base	Width of base
		Liomys irroratus		
N	10	10	10	10
Mean	8.2	27.4	1.73	1.60
Minimum	7.5	24.8	1.45	1.30
Maximum	9.6	28.9	1.90	1.75
1 SE	± 0.20	± 0.42	± 0.04	± 0.04
		Liomys pictus		
N	10	10	10	10
Mean	8.7	31.0	1.46	1.21
Minimum	7.5	26.1	1.15	0.90
Maximum	10.2	36.4	1.75	1.50
1 SE	± 0.25	± 1.10	± 0.05	± 0.07
		Liomys spectabilis		
KU 96037	9.1	30.3	1.50	1.10
KU 96044	9.8	32.7	1.70	1.55
		Liomys salvini		
N	10	10	10	10
Mean	7.9	28.6	1.53	1.36
Minimum	6.9	25.7	1.25	1.15
Maximum	9.1	32.5	1.70	1.55
1 SE	± 0.25	± 0.69	± 0.04	± 0.03
		Liomys adspersus		
KU 121532	8.9	26.2	1.70	1.50
KU 121533	10.0	32.2	1.80	1.70
		Heteromys gaumeri		
KU 92130	8.1	23.8	1.65	1.25
KU 92136	8.8	25.1	1.75	1.45
		Heteromys desmarestianus		
KU 71257	8.8	23.8	1.55	1.55

height of the base (1.53) and the average width (1.36) also are in the middle of the range of variation of species studied.

From the base, the shaft tapers steeply at first and then more gradually. The slope near the base is not as steep as seen in the baculum of *L. irroratus*. Near the upturned tip of the baculum of *Liomys salvini*, the shaft is dorsoventrally flattened. At this point the shaft is somewhat expanded laterally, giving the bone the appearance of an arrowhead in dorsal view (Fig. 56C). The dorsoventral flattening and lateral expansion of the baculum near its tip serves to distinguish *L. salvini* from all other species studied except *L. adspersus.*

Liomys adspersus (Fig. 56D).—The baculum of this species closely resembles that of *L. salvini.* Although the baculum of *adspersus* is actually somewhat larger than that of *salvini,* it is proportionally no longer when compared with overall body size. In the two available specimens, the dorsoventrally flattened area near the tip of the shaft does not flair laterally so much as in *L. salvini* and the tip does not turn upward to the same degree.

Heteromys desmarestianus (Fig. 56F).—The baculum of this species and of *Heteromys gaumeri* are, in comparison to body size, much shorter than the bacula of any species of *Liomys.* In the one specimen of *H. desmarestianus* studied, the base is as wide as it is high.

The morphology of the baculum of *H. desmarestianus* is indistinguishable from that of *Liomys irroratus.* The base occupies about one-third the total length of the bone. The remainder of the shaft tapers gradually to the slightly upturned tip. The extreme tip of the shaft may be laterally compressed, but the area is not extensive. The shaft is otherwise oval in outline.

Heteromys gaumeri (Fig. 56G).—The baculum of this species is similar to that of *Heteromys desmarestianus.* However, the shaft is smaller in diameter, in some specimens almost needle-like. The tip is slightly upturned, but there is no evidence of lateral flattening at the tip in any of the specimens studied. The shaft is essentially oval in outline throughout its length.

Conclusions.—The bacula of the seven species studied appear to fall into three distinct groups. The group with the least complex structure is represented by *Liomys irroratus, Heteromys desmarestianus,* and *Heteromys gaumeri.* In these three species, the shaft of the baculum is oval throughout its length, although the tip may be somewhat compressed laterally. A second group is formed by *Liomys salvini* and *Liomys adspersus,* in which the baculum is dorsoventrally flattened near the end of the shaft; also the shaft is laterally expanded in the flattened area. The most complex bacular morphology obtains in *Liomys pictus* and *Liomys spectabilis.* The bacula of these two species have a ventral keel at the tip, which is laterally compressed, and, just posterior to the keel, the shaft has been dorsoventrally flattened and the shaft is flared laterally. Specimens examined in studying bacular morphology are listed below.

Liomys irroratus.—1 mi. N Chorro, Durango, 1 (KU 49005); Omilteme, Guerrero, 1 (KU 98762); Belén del Refugio, Jalisco, 1 (KU 103781); 2 6/10 mi. E Etzatlán, Jalisco, 1 (KU 96024); 3½ mi. WNW Zapoltitic, Jalisco, 1 (KU 97193); 3 mi. ESE Oaxaca, Oaxaca, 1 (KU 61602); 3 mi. N Izúcar de Matamoros, Puebla, 1 (KU 62613); 6½ mi. SW Izúcar de Matamoros, Puebla, 1 (KU 67715); 1 mi. S Altamira, Tamaulipas, 1 (KU 55957); Soto la Marina, Tamaulipas, 1 (KU 55885).

Liomys pictus.—Finca San Salvador, 15 km. SE San Clemente, Chiapas, 1 (KU 102639); 5 km. N Agua del Obispo, Guerrero, 1 (KU 99807); 2 2/10 mi. NE Contla, Jalisco, 2 (KU 96062-63); 3½ mi. WNW Zapoltitic, Jalisco, 1 (KU 97195); 2 mi. SW Rosamorada, Nayarit, 1 (KU 61629); 20 mi. S, 5 mi. E Sola de Vega, Oaxaca, 1 (KU 98768); 10 mi. W, 2 mi. N Tehuantepec, Oaxaca, 1 (KU 54698); 18 km. NNW Choix, Sinaloa, 1 (KU 89468); Río Blanco, 20 km. WNW Piedras Negras, Veracruz, 1 (KU 17941).

Liomys spectabilis.—8 km. N Contla, Jalisco, 1 (KU 96037); 3 3/10 mi. NE Contla, Jalisco, 1 (KU 96044).

Liomys salvini.—1 mi. NW San Salvador, El Salvador, 2 (KU 71077, 71086); 1 mi. SE Monogoy, Guatemala, 1 (KU 71068); 1 mi. SE Puerto Madero, Chiapas, 1 (KU 68850); 6 mi. NW Tonalá, Chiapas, 1 (KU 68839); 4 km. S, 1½ km. E Alta Gracia, Nicaragua, 1 (KU 115389); 3 km. N, 4 km. W Diriamba, Nicaragua, 1 (KU 110442); 1 km. NE Esquipulas, Nicaragua, 1 (KU 115371); Hda. Bellavista, Nicaragua, 1 (KU 106488); 3 mi. SW Managua, Nicaragua, 1 (KU 71164).

Liomys adspersus.—2 km. NE Buenos Aires, Panamá, 2 (KU 121532-33).

Heteromys desmarestianus.—5 mi. S, 2 mi. E Jinotega, Nicaragua, 1 (KU 71257).

Heteromys gaumeri.—1½ km. S, 1 km. E Pueblo Nuevo X-can, Quintana Roo, 1 (KU 92136); 2 km. N Pisté, Yucatán, 1 (KU 92130).

Morphology of Spermatozoa

Almost nothing is known about the spermatozoa of free-living mammals; Forman (1968) presented a review of the scanty literature dealing with the use of sperm morphology in systematics. I have been able to obtain spermatozoa of the five species of *Liomys* for study, but have been unable to obtain material of *Heteromys*. I have seen, however, spermatozoa of another heteromyid genus, *Perognathus*, which will be discussed briefly.

To obtain spermatozoa, the epididymis of freshly-killed specimens was removed; a small amount of the fluid containing mature sperm was taken and suspended in an isotonic solution of sodium citrate. A few drops of the sodium citrate and spermatozoan solution were placed on a microscope slide and allowed to air dry. Dilution of the spermatozoa with sodium citrate was necessary so that individual spermatozoa would be dispersed for study and photographing. Spermatozoa were fixed with a solution of one part acetic acid and four parts absolute methyl alcohol. Sperms were stained for 30 minutes with a 0.02 solution of toluidine blue in water. All observations were made using a Leitz Ortholux Research Microscope at a magnification of 950. Measurements were taken by means of dial calipers from the direct contact prints (4 × 5 inches) from the negatives. On the prints, 1.25 millimeters equaled one micron. Measurements follow those used by Forman (1968:904).

Liomys irroratus (Fig. 57A).—Head is long and has a rounded point at the apex. The base of the head is smoothly rounded with the exception of a notch on one side. The broadest part of the head is just anterior to the notch. No neck was observed between the head and midpiece in this species; this could be the result of preparation or staining techniques, but a distinct neck was observed in the four other species studied. The head of the sperm of *irroratus* is significantly (Student's *t*-test, at 0.05) broader than in *L. pictus* (Table 40). There was no significant difference in other measurements between *irroratus* and *pictus* or *spectabilis* (the two species with spermatozoa that most closely resemble that of *irroratus*).

Liomys pictus (Fig. 57B).—The head is long and has an acutely pointed apex. Although the head of the sperm of *pictus* generally resembles that of *irroratus*, the apex of the head is more sharply pointed in *pictus*. The base of the sperm of *pictus* is flatter and less rounded than in *irroratus*, although the notch at one side

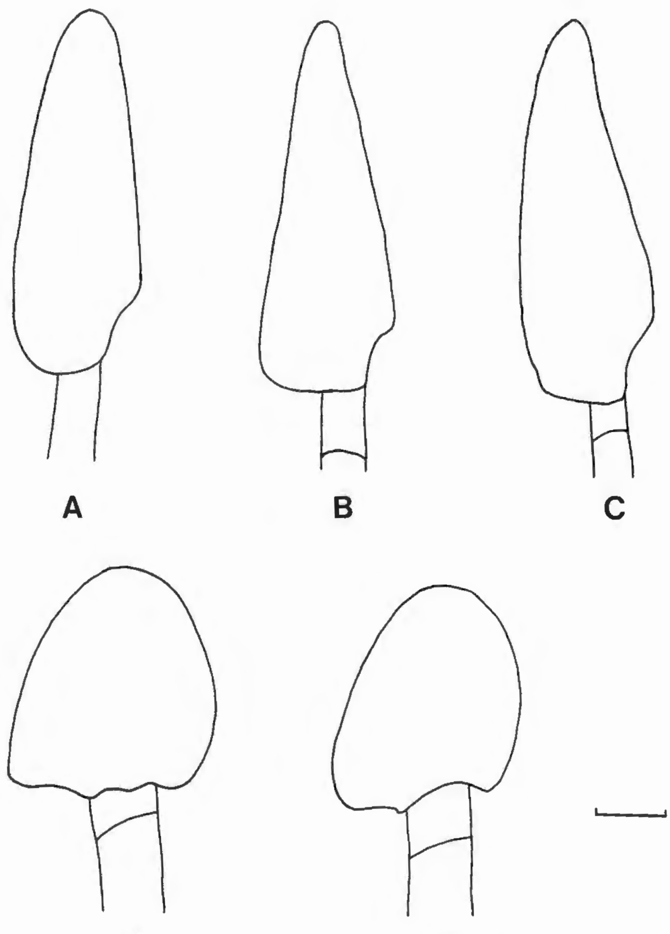


FIG. 57.—Head and neck region of spermatozoa of five species of *Liomys*. The species are A, *Liomys irroratus* (TTU 9868); B, *Liomys pictus* (KU 120592); C, *Liomys spectabilis* (KU 120606); D, *Liomys salvini* (KU 120597); E, *Liomys adspersus* (KU 121527). The scale at the lower right is one micron long.

of the base is present. The broadest portion of the head is just anterior to the notch. A neck is clearly present in this species.

Liomys spectabilis (Fig. 57C).—The morphology of the spermatozoa of this species closely resembles that found in *Liomys pictus*, although the head is significantly longer and broader than in *pictus* (Table 40). The base of the head is not as squared as in *pictus* and the broadest portion of the head is farther anterior of the notch than in that species. A distinct neck is present. There is no significant difference in the length of the neck between *spectabilis* and *pictus*.

Liomys salvini (Fig. 57D).—The head of the sperm of this species is short, being broadest in the basal region and bluntly rounded at the apex. The base is relatively smooth, showing some minor irregularities that are individually

TABLE 40.—*Measurements (in microns) of the head and neck of the spermatozoa of five species of* Liomys. *All samples were based on 10 spermatozoa.*

Statistics	Length of head	Width of head	Length of neck
		Liomys irroratus	
Mean	5.35	1.97	
Range	(4.95-5.78)	(1.73-2.27)	
1 SE	± 0.067	± 0.048	
		Liomys pictus	
Mean	5.22	1.81	0.74
Range	(4.81-5.46)	(1.67-1.99)	(0.53-0.98)
1 SE	± 0.062	± 0.032	± 0.046
		Liomys spectabilis	
Mean	5.56	2.07	0.62
Range	(5.23-5.95)	(1.90-2.28)	(0.43-0.81)
1 SE	± 0.074	± 0.042	± 0.040
		Liomys salvini	
Mean	3.22	2.97	0.54
Range	(3.05-3.35)	(2.67-3.19)	(0.33-0.69)
1 SE	± 0.037	± 0.052	± 0.042
		Liomys adspersus	
Mean	3.17	2.80	0.75
Range	(3.00-3.32)	(2.57-3.06)	(0.60-0.88)
1 SE	± 0.030	± 0.046	± 0.028

variable. No notch is evident on a side of the base. A neck is present between the head and midpiece.

Liomys adspersus (Fig. 57E).—The morphology of the head of the spermatozoa of *adspersus* is similar to that of *salvini*. The base is slightly concave at the point of attachment of the neck. Although there is no significant difference in the length of the head of *salvini* and *adspersus*, that of *salvini* is significantly broader than in *adspersus* (Table 40), and the neck of the sperm of *adspersus* is significantly longer than the neck in *salvini*.

Conclusions.—In the spermatozoa of *Liomys* that I have examined, there appear to be two basic morphological types; one type is long and pointed and the other is short and blunt. The first type of sperm is found in *L. irroratus*, *L. pictus*, and *L. spectabilis*. Within this group, *irroratus* can be distinguished from the other two species because it lacks a neck between the head and midpiece and also because the apex and base of the head are more rounded. The other two species—*pictus* and *spectabilis*—can be distinguished only on the basis of mensural data.

The second type of sperm morphology is represented by *Liomys salvini* and *Liomys adspersus*. I cannot with any accuracy distinguish between the sperm of

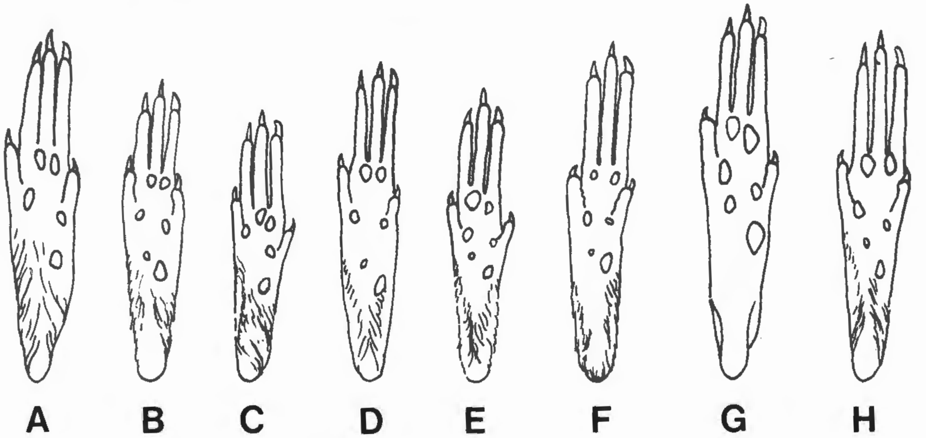


FIG. 58.—Semi-schematic drawings of the hind feet of five species of *Liomys* (two are shown for *pictus*) and two species of *Heteromys* illustrating the number and positioning of plantar tubercles and amount of hair on soles. The species are as follows: A, *Liomys irroratus* (KU 14706); B, *Liomys pictus* (KU 94506); C, *Liomys pictus* (KU 120591); D, *Liomys spectabilis* (KU 96045); E, *Liomys salvini* (KU 120605); F, *Liomys adspersus* (KU 121531); G, *Heteromys desmarestianus* (KU 84370); H, *Heteromys gaumeri* (KU 92127). The scale at the right is 10 millimeters long.

these two species based upon qualitative characters, but they can be distinguished by quantitative characteristics.

Unfortunately, spermatozoa of a species of *Heteromys* are not available for study at present; however, I have examined the spermatozoa of a specimen (KU 120581) of *Perognathus pernix*. The sperm of this species most closely resembles that of the first group of *Liomys* (*irroratus*, *pictus*, and *spectabilis*). Based on this meager information, I suppose that the type of sperm morphology found in these three species represents the more primitive type, whereas that found in *L. salvini* and *L. adspersus* is the derived type. Specimens examined are listed below.

Liomys irroratus.—La Cienegilla Springs, 46.9 mi. S Jiménez, Chihuahua, 1 (TTU 9868); 2½ mi. SE Altamira, Tamaulipas, 1 (TTU 9869). *Liomys pictus.*—2 km. NW Emiliano Zapata, Jalisco, 1 (KU 120587); 4 km. W Tuxpan, Jalisco, 2 (KU 120592, 120594). *Liomys spectabilis.*—6 km NE Contla, Jalisco, 1 (KU 120606). *Liomys salvini.*—16 km. SW Tapachula, Chiapas, 2 (KU 120597, 120600). *Liomys adspersus.*—2 km. NE Buenos Aires, Panamá, 2 (KU 121527-28).

MORPHOLOGY OF THE HIND FOOT

The first superspecific grouping of the members of the genus *Heteromys* (including species presently regarded as members of the genus *Liomys*) was proposed by Thomas (1893*a*:330) and expanded by J. A. Allen (1897:57). This classification was based solely upon the morphology of the hind feet; characters employed were number of plantar tubercles and whether or not the soles of the feet were hairy. Three groups of species were recognized—those with five plantar tubercles and hairy soles, those with six plantar tubercles and hairy soles, and those with six plantar tubercles and naked soles. With few exceptions, this is still a relatively useful method for grouping members of the two genera.

Plantar tubercles (Fig. 58).—All species of the genus *Liomys* have six plantar tubercles on each hind foot except *Liomys irroratus* (Fig. 58A) and one small population of *Liomys pictus* (Fig. 58C) in which there are five. Also all members of the genus *Heteromys* possess six plantar tubercles. The tubercle apparently absent in *irroratus* is the small tubercle slightly anterior and external to the large, posteriormost tubercle in other species. It is this tubercle that is variable also in populations of *Liomys pictus plantinarensis*, especially those in southeastern Jalisco. It is absent in some specimens from this area, represented by a small pigmented spot in others, and well developed in still others (see account of *L. p. plantinarensis* for details).

Sole of feet (Fig. 58).—The soles of the hind feet of all members of the genus *Liomys* are haired. All members of the genus *Heteromys* except *Heteromys gaumeri* (Fig. 58H) have the soles of the hind feet that are naked.

Conclusions.—The species in these two genera can be divided into the three groups recognized by Thomas and Allen. *Liomys irroratus* is the only species characterized by five plantar tubercles and hairy soles on the hind feet. The remaining four species of *Liomys* (*pictus*, *spectabilis*, *salvini*, and *adspersus*) and *Heteromys gaumeri* are characterized by possession of six plantar tubercles and hairy soles. The other species in the genus *Heteromys* have six plantar tubercles and the soles of the hind feet that are naked (see Goldman, 1911:15).

These data are based upon examination of numerous specimens, both dried skins and those preserved in alcohol, as well as field observations made by several collectors (including myself) on fresh material.

Comparative Karyology

The only literature reference to the karyotype of a heteromyine rodent is Makino's (1953) erroneous report of the diploid number in *Liomys irroratus* being 58. As will be seen below, the 2N of *irroratus* is 60 with many pairs of small telocentric chromosomes, one of which probably was not seen by Makino.

Chromosome preparations were made from bone marrow cells using a flame-dry technique modified from Patton (1967) and Lee (1969). Preparations were stained in a saturated solution of crystal violet. Results discussed below are based on the study of at least five cells (usually 10) from each individual. Some cells had less than the modal number of chromosomes for the species, but this difference undoubtedly resulted from loss of chromosomes during preparation. Cells having less than the modal number for the species were not included in the counts.

Liomys irroratus.—This species is characterized by diploid number of 60 (Fig. 59 and Table 41), including one medium-sized pair of metacentrics, one pair of large submetacentrics, and 27 pairs of telocentrics. The X-chromosome is a large submetacentric and the Y-chromosome is a medium-sized subtelocentric. The fundamental number exclusive of the sex chromosomes is 62.

Liomys pictus.—A diploid number of 48 (Fig. 59 and Table 41), characterizes *pictus* and includes five pairs of metacentrics, five pairs of submetacentric to

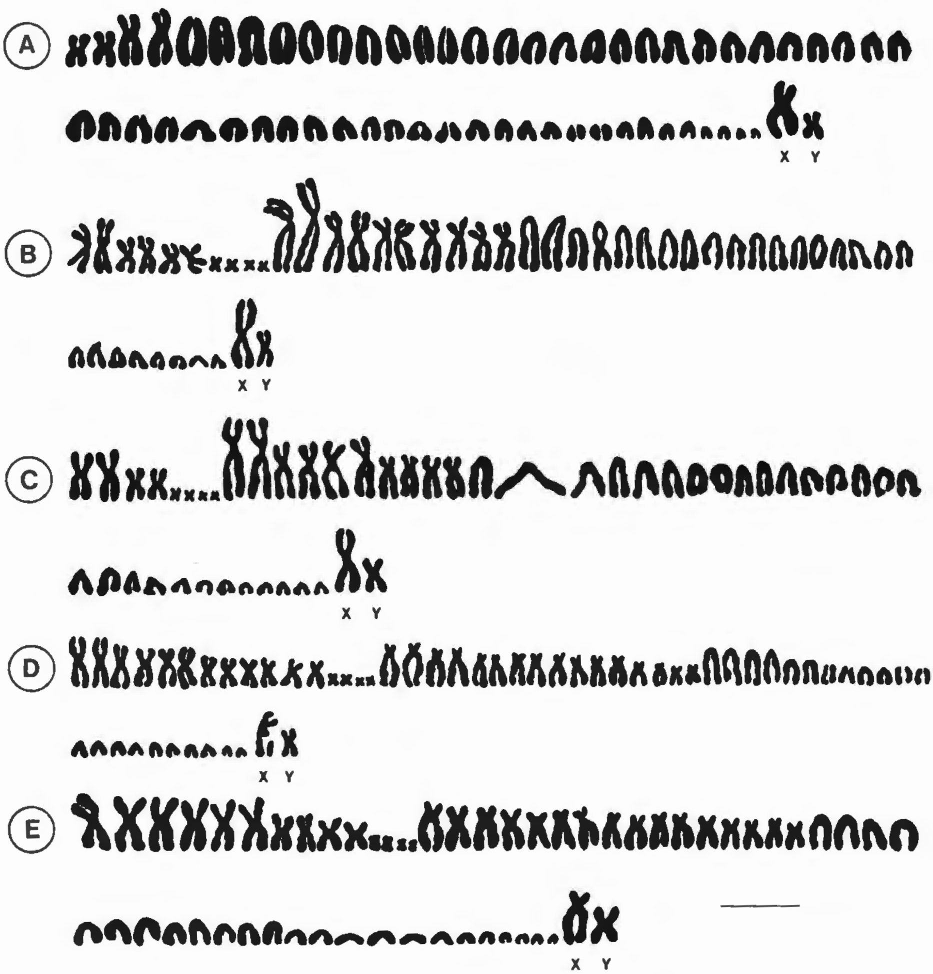


FIG. 59.—Karyotypes of males of five species of *Liomys*. The species are as follows: A, *Liomys irroratus*; B, *Liomys pictus*; C, *Liomys spectabilis*; D, *Liomys salvini*; E, *Liomys adspersus*. The scale at the lower right is 10 microns long.

subtelocentrics, and 13 pairs of telocentrics. The X-chromosome is a large metacentric and the Y-chromosome is a medium-sized metacentric. The fundamental number is 66.

Liomys spectabilis.—This species has a diploid number of 48 (Fig. 59 and Table 41), including four pairs of metacentrics, five pairs of submetacentric to subtelocentrics, and 14 pairs of telocentrics. The X-chromosome is a large metacentric and the Y-chromosome is a medium-sized metacentric. The fundamental number is 64.

Liomys salvini.—The diploid number of *salvini* is 56 (Fig. 59 and Table 41), including eight pairs of metacentrics, eight pairs of submetacentric-subtelocentrics, and 11 pairs of telocentrics. The X-chromosome is a large sub-

TABLE 41.—*Somatic chromosome numbers and morphological types of five species of* Liomys *and one species of* Heteromys. *FN=fundamental number, M=metacentric, SM-ST=submetacentric-subtelocentric, T=telocentric.*

			Autosomes				
Species	2n	FN	M	SM-ST	T	X	Y
Liomys pictus	48	66	5	5	13	Large M	Medium M
Liomys spectabilis	48	64	4	5	14	Large M	Medium M
Liomys salvini	56	86	8	8	11	Large SM	Medium M
Liomys adspersus	56	84?	7?	8	12	Large SM	Medium M
Liomys irroratus	60	62	1	1	27	Large SM	Medium ST
*Heteromys desmarestianus**	60	82	0	12	17	Large SM	?

*Information supplied by A. L. Gardner

metacentric and the Y-chromosome is a medium-sized metacentric. The fundamental number is 86.

Liomys adspersus.—This species has a diploid number of 56 (Fig. 59 and Table 41) including probably seven pairs of metacentrics, eight pairs of submetacentric to subtelocentrics, and 12 pairs of telocentrics. Because chromosome preparations for this species were not satisfactory, I was unable to discern whether two small pairs of chromosomes were metacentrics or telocentrics. I have counted these as metacentric chromosomes corresponding to the two small pairs seen in *salvini*, but this is a tentative assignment. The X-chromosome is a large submetacentric and the Y-chromosome is a medium-sized metacentric. The fundamental number is 84 (or, if the two small pairs were telocentrics, 80).

Heteromys desmarestianus.—Data for this species were supplied by Dr. A. L. Gardner. The diploid number is 60 (Table 41), with no metacentric pairs, 12 submetacentric to subtelocentric pairs, and 17 telocentric pairs. The X-chromosome is a large submetacentric, but I have no information on the Y-chromosome. The fundamental number is 82.

Conclusions.—Based on diploid number, the karyotypes of the six species can be divided into three groups. *Liomys irroratus* and *Heteromys desmarestianus* had a diploid number of 60, although *desmarestianus* had a much higher fundamental number differing from *irroratus* by 10 pericentric inversions. Specimens of *Liomys salvini* and *Liomys adspersus* had a diploid number of 56 and differed by at least a pericentric inversion. *Liomys pictus* and *Liomys spectabilis* both had a diploid number of 48, but differed by a single pericentric inversion.

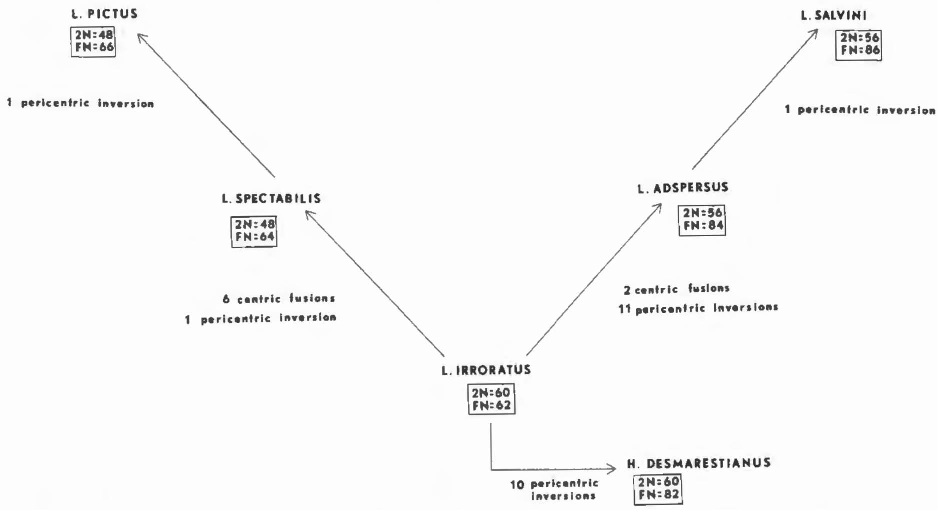


FIG. 60.—Hypothetical pathways for chromosomal evolution in five species of *Liomys* and one of *Heteromys*. This is the most parsimonious arrangement based upon the assumption that *Liomys irroratus* possesses the most primitive karyotype.

In order to gain some insight into the possible direction of chromosomal evolution in this group, it is necessary to attempt to identify the primitive karyotype of the genus. The characteristics of a "primitive" karyotype for mammals have been considered by several authors (Klinger, 1963; Hamerton *et al.*, 1963) to be a high diploid number and numerous telocentrics. This is based upon the assumption that in mammals the main mechanism for changing chromosomal numbers has been centric fusion (Hsu and Mead, 1969; Matthey, 1958; Nadler, 1966, 1969), although there is growing evidence for centric fission in at least some groups (Hoffmann and Nadler, 1968). Following the classical interpretation, *Liomys irroratus* would be considered as having the most primitive karyotype for the heteromyine rodents examined. This species has, along with *Heteromys desmarestianus*, the highest diploid number of the six species studied and has a high number (27) of telocentric chromosomes. (Aside from this evidence *Liomys irroratus* seems to have retained more primitive characteristics in other characters studied than have other members of the genus *Liomys*.) Also, sharing a diploid number of 60 with *Heteromys desmarestianus* suggests that the primitive diploid number for the Heteromyinae was 60, although final assessment of this possibility must await more data concerning the karyology of other members of the genus *Heteromys*. I can find no objections to considering *Liomys irroratus* as having the most primitive chromosomal compliment in the genus.

If the assumption of *Liomys irroratus* having the "primitive" chromosomal compliment is accepted, then possible pathways for derivation of the chromosomal compliments of other members of the genus can be constructed (Fig. 60). My arrangement should not be construed as being the only possible solution to the problem, but I do believe it is the most parsimonious on the basis of the original assumption. From the karyotype of *Liomys irroratus*, that of *Heteromys* *desmarestianus* can be derived by 10 pericentric inversions. To derive the chromosomal compliments of *Liomys adspersus* from that of *Liomys irroratus* would require two centric fusions and 11 pericentric inversions and to obtain the chromosomal compliment of *Liomys salvini* would require one additional pericentric inversion. On the other hand, to obtain the karyotype of *Liomys spectabilis* from *Liomys irroratus* would require six centric fusions and one pericentric inversion and to obtain the karyotype of *Liomys pictus* would require only one additional pericentric inversion. The split into a *pictus*-line and *salvini*-line may not have been directly from *irroratus*, because a mouse with two centric fusions and one pericentric inversion beyond the chromosomal compliment of *irroratus* would still be basic to both lines; nevertheless, beyond such a point a split into the two lines would seem to be the most logical explanation. It is of interest to note that the *salvini*-line appears to have emphasized pericentric inversions in the evolution of its chromosomes, whereas the *pictus*-line appears to have emphasized centric fusions. Specimens examined from which karyotypic material was available are as follows.

Liomys irroratus.—La Cienegilla Springs, 46.9 mi. S Jiménez, Chihuahua, 1 (TTU 9868); 5 km. N San José, Guanjuato, 3 (WBC 866-868); Omilteme, Guerrero, 1 (KU 120582); 12 km. N Cd. Victoria, Tamaulipas, 1 (WBC 865); 5 mi. SE Brownsville, Cameron Co., Texas, 2 (TTU 9857-58).

Liomys pictus.—4 km. NE Contla, Jalisco, 1 (KU 120590); 2 km. NW Emiliano Zapata, Jalisco, 1 (KU 120587); Río Cuchajaqui, 8 mi. S Alamos, Sonora, 1 (supplied by J. L. Patton).

Liomys spectabilis.—6 km. NE Contla, Jalisco, 1 (KU 120606).

Liomys salvini.—16 km. SW Tapachula, Chiapas, 2 (KU 120597, 120600); no specific locality, Nicaragua, 1 (supplied by J. L. Patton).

Liomys adspersus.—2 km. NE Buenos Aires, Panamá, Panamá, 3 (KU 121528-30).

Ectoparasites

The list of ectoparasites for species of *Liomys* and *Heteromys* given in Appendix II and the discussion below are based primarily upon two sources of information—a compilation of all records in the published literature and ectoparasites collected during field work under a contract (DA-49-193-MD-2215) to Dr. J. Knox Jones, Jr., from U.S. Army Medical Research and Development Command and identified by experts on the various taxonomic groups (listed in Acknowledgments). The latter records are indicated in Appendix II by numbers, which correspond to numbered localities of capture for the host given at the end of the list.

Liomys irroratus.—Twenty-two species of mites, of which 17 are trombiculids, three laelapids, and two macronyssids, have been found on specimens of *Liomys irroratus.* Of these 22 species, eight have been reported also from *pictus* (*Ectomyx fusicornis, Euschoengastia gagarini, Eutrombicula alfreddugesi, Leptotrombidium panamense, Pseudoschoengastia audyi, P. hoffmannae, P. hungerfordi,* and *Steptolaelaps liomydis*), two from *salvini* (*Eutrombicula alfreddugesi* and *Leptotrombidium panamense*), three from *adspersus* (*Androlaelaps fahrenholzi, Leptotrombidium panamense,* and *Ornithonyssus bacoti*), and two from *Heteromys desmarestianus* (*Androlaelaps fahrenholzi* and *Eutrombicula* *alfreddugesi*). Two species of ticks have been found on *L. irroratus* of which one, *Ixodes eadsi*, has also been reported from *L. salvini*. Two species of lice and three of fleas are known from this spiny pocket mouse; two of the fleas (*Polygenis gwyni* and *P. martinezbaezi*) also have been reported from *Liomys pictus*.

Liomys pictus.—Of the 23 species of mites known to occur on *Liomys pictus*, 20 are trombiculids and three are laelapids. *L. pictus* had three species of mites in common with *L. salvini* (*Eutrombicula alfreddugesi*, *Leptotrombidium panamense*, *Steptolaelaps heteromys*), two in common with *L. adspersus* (*Leptotrombidium panamense* and *Steptolaelaps heteromys*), and two in common with *Heteromys desmarestianus* (*Eutrombicula alfreddugesi* and *Steptolaelaps heteromys*). Only one species of tick, *Ixodes sinaloa*, is known from this species; this tick also has been reported from *L. salvini*. One species of louse and five of fleas are known from *L. pictus* and of these species, one flea (*Polygenis vulcanius*) is known also from *L. salvini* and two fleas are known from *L. irroratus* (see above).

Liomys salvini.—Sixteen species of mites (11 trombiculids and five laelapids) are presently known from this Middle American species of *Liomys*. Of these 16 species, four have been reported also from *L. adspersus* (*Ascoschoengastia dyscrita*, *Eutrombicula goeldii*, *Leptotrombidium panamense*, and *Steptolaelaps heteromys*) and five have been reported from *Heteromys desmarestianus* (*Ascoschoengastia dyscrita*, *Eutrombicula alfreddugesi*, *Eutrombicula goeldii*, *Trombicula dunni*, and *Steptolaelaps heteromys*). Two species of ticks and one flea are known from this species. The one species of louse, *Fahrenholzia fairchildi*, known from *L. salvini* also has been reported from *L. adspersus* and *Heteromys desmarestianus*.

Liomys adspersus.—Fourteen species of mites (10 trombiculids, three laelapids, and one macronyssid) have been reported thus far from this Panamanian pocket mouse. Seven of these 14 species are known also from *Heteromys desmarestianus* (*Androlaelaps fahrenholzi*, *Ascoschoengastia dyscrita*, *Eutrombicula goeldii*, *Pseudoschoengastia bulbifera*, *P. tricosa*, *Hirstionyssus microchelae*, and *Steptolaelaps heteromys*). An unspecified species of the genus *Amblyomma* is the only tick reported from *adspersus*; one louse, *Fahrenholzia fairchildi*, also known from *L. salvini* and *H. desmarestianus* has been recorded from *adspersus*. Of the three species of fleas taken from this species, none has been reported from the other four species of mice presently under consideration, but one (*Polygenis dunni*) has been taken on *Heteromys anomalus* and another (*Polygenis klagesi*) is known from *Heteromys australis*.

Heteromys desmarestianus.—The occurrence of 26 species of mites (16 trombiculids, nine laelapids, and one speleognathid) has been reported from *Heteromys desmarestianus*. No records of ticks are available for this species. Three species of lice and five species of fleas from three families have been taken from specimens of *Heteromys desmarestianus*.

Conclusions.—Because some of the life stages of trombiculid mites and argasid and ixodid ticks are free-living away from vertebrate hosts, these taxa are of relatively little use in elucidating phylogenetic relationships of their hosts.

However, when sufficient information becomes available about the ecology of these parasites, differences in the composition of the trombiculid mite and tick faunas may give insight into ecological differences of their hosts.

As pointed out by Wenzel and Tipton (1966:699), genera of laelapid mites exhibit a striking host association at the supergeneric level. Members of genus *Eubrachylaelaps* were found primarily on peromyscine cricetid rodents; the genera *Laelaps* and *Gigantolaelaps* were primarily taken from complex-penis-type cricetine rodents. The principal hosts of the genus *Tur* were caviomorph rodents. Members of the genus *Steptolaelaps* were restricted to heteromyid rodents. Two genera, *Androlaelaps* and *Hirstionyssus*, have a wider host tolerance in that members of the former genus are found on a wide variety of mammalian hosts and representatives of the latter primarily on heteromyid, cricetid, and sciurid rodents.

Because fleas are somewhat more closely tied to their mammalian hosts, it was hoped that members of this group might reveal useful information concerning members of the genera *Liomys* and *Heteromys*. At first glance, there appears to be little overlap in the associated species of fleas between these spiny pocket mice. However, further examination reveals that, in most cases, heteromyid rodents are only incidental hosts and that other mammals are the primary hosts of the listed fleas. The only possible exception may be *Polygenis dunni*, of which more specimens were taken in Panamá from *Liomys adspersus* than from any other host (Tipton and Méndez, 1966:298), and the two species of *Wenzella*, which are known only from *Heteromys desmarestianus*. Dr. Robert Traub after reviewing my list of fleas occurring on *Liomys* and *Heteromys* made the following statement in a letter (4 May 1971) to J. Knox Jones, Jr.: ". . . it is important to note that various species of *Polygenis* that are listed for *Liomys* actually infest many other hosts and are generally far more abundant on such rodents than on *Liomys*. Of all the fleas listed in my records from *Liomys*, I doubt that there is one that is specific or even characteristic. My own records of fleas from *Heteromys* are virtually nil, but the species of *Wenzella* are the only ones listed. . . that fall in the category of *Heteromys*-fleas, and these are nest-inhabiting species."

One group that does offer some evidence on possible phylogenetic relationship of their hosts are the anopluran lice of the genus *Fahrenholzia*. Lice are highly host-specific, passing all life stages on their host and resisting even host-to-host transfer unless there is intimate contact. Species of *Fahrenholzia* occur only on heteromyid rodents; fortunately, this genus of lice has received recent taxonomic study by Stojanovich and Pratt (1961) for the four species occurring on members of the subfamilies Dipodomyinae and Perognathinae, and by Johnson (1962) for the "*microcephala* group" that occurs on members of the subfamily Heteromyinae.

Of the seven species of the "*microcephala* group," five are known from a single species of *Liomys* or *Heteromys* (Table 42). The remaining two species, *fairchildi* and *ferrisi*, each have been reported from three hosts; specimens of *fairchildi* are known from *L. salvini*, *L. adspersus*, and *Heteromys desmarestianus*,

TABLE 42.—*Distribution of species of the anopluran genus* Fahrenholzia *on their mammalian hosts of the genera* Liomys *and* Heteromys.

Host species	*F. ehrlichi*	*F. fairchildi*	*F. ferrisi*	*F. hertigi*	*F. microcephala*	*F. schwartzi*	*F. texana*
Liomys irroratus	+						+
Liomys pictus					+		
Liomys spectabilis							
Liomys salvini		+					
Liomys adspersus		+					
Heteromys anomalus						+	
Heteromys desmarestianus		+	+	+			
Heteromys gaumeri			+				
Heteromys goldmani			+				

and specimens of *ferrisi* are known from three species of *Heteromys* (*desmarestianus*, *gaumeri*, and *goldmani*). Because *fairchildi* is the only species known from *L. salvini* and *L. adspersus* and *ferrisi* is the only species known from *H. goldmani* and *H. gaumeri*, it would appear highly probable that these species of lice evolved on one or both of these hosts and subsequently dispersed to *Heteromys desmarestianus*. *Fahrenholzia hertigi* is known only from *H. desmarestianus* and is most likely the species that has evolved on this host.

Only two hosts are known to harbor more than one species of *Fahrenholzia*. *Liomys irroratus* is the only known host of *F. ehrlichi* and *F. texana*; as pointed out above, three species (*fairchildi*, *ferrisi*, and *hertigi*) have been recorded for *Heteromys desmarestianus*, although only *hertigi* is unique to that species.

ENDOPARASITES

Little information has been recorded concerning the endoparasites of heteromyine rodents; all records available were found coincidental to studies of human diseases or in general surveys for a particular type of parasite.

Two species of Coccidia, *Eimeria liomysis* and *Eimeria picti*, have been described from *Liomys pictus* from Sinaloa and Nayarit and from *Liomys irroratus* from Jalisco (Levine *et al.*, 1958; Ivens *et al.*, 1959). These protozoan parasites were recovered from fecal samples of these two species of mice. Esquivel-R. *et al.* (1967:954) described *Trypanosoma zeledoni* based on blood smears prepared from specimens of *Liomys salvini* from Costa Rica. During a survey for possible reservoir hosts of leishmaniasis in the vicinity of Roaring River, Cayo, British Honduras, *Leishmania mexicana* was isolated from cutaneous lesions on the tails of six of 58 specimens of *Heteromys desmarestianus* (Lainson and

Strangway-Dixon, 1964*a*:3, 1964*b*:146-147). The only other rodents from which *Leishmania* was identified were *Ototylomys phyllotis* and *Nyctomys sumichrasti*, which also had cutaneous lesions on their tails. Leishmaniasis has been reported from the human population of this area of British Honduras, but only from people who lived or worked in heavily forested areas. Disney (1964:581) reported a specimen of *Heteromys desmarestianus* from Spanish Lookout, Cayo, British Honduras, with a heavy infestation of leishmaniasis on its ears, and upon post-mortem examination was found to have visceral involvement of the liver, spleen, and lungs.

Caballero y Caballero (1959) reported specimens of two species of nematodes, *Trichuris* sp. and *Longistriata vexillata*, from specimens of *Liomys salvini* taken in the vicinity of Mapastepec, Chiapas. Hookworms were observed in the duodenum of two specimens of *Heteromys desmarestianus* from the vicinity of Palenque, Chiapas, by Kuns and Tashian (1954:101).

No bacterial or viral diseases have been reported from species of either *Liomys* or *Heteromys*, although 51 specimens of *Liomys salvini* were examined during a leptospirosis survey in Nicaragua (Clark *et al.*, 1966).

Reproduction

Reproductive data presented herein that were not drawn from the published literature are based upon information recorded on specimen labels or in the field notes of the collector. Although data were recorded from specimens in most museums visited, the bulk of the data are from material housed in the Museum of Natural History at The University of Kansas. Females here recorded as non-pregnant were only those that were so noted by the collector.

Liomys irroratus.—Of the 281 adult females of this species examined for which reproductive data were available, 52 were gravid and 12 were lactating. Pregnant females were recorded for all months except February, April, and June, and in one of these months, June, a lactating female was taken. The peak reproductive activity appears to be in the months of August to November when over a third of the females were pregnant in each month (Table 43). The mean number of embryos per female was 4.39 (mode four) with a range of two to eight. Males with enlarged testes were collected in each of the eight months (Table 43) for which data are available.

Some data reported herein were recorded earlier by Dalquest (1953:122), Hall and Dalquest (1963:285), and Alvarez (1963:433). Davis (1944:389) recorded a female of *L. i. guerrerensis* from 15 km. SW Chilpancingo, Guerrero, that was found to be gravid on August 17 (no embryo count given), and Koestner (1941: 12) obtained a female on an unspecified date at Ojo de Agua, Nuevo León, that carried five embryos. Fleming (1969) reported immature individuals of *Liomys irroratus* from all months except May; he believed that *irroratus* breeds throughout the year, but with a peak from November to February.

Liomys pictus.—Forty-nine of the 284 females with reproductive data were noted as being pregnant and an additional 11 were lactating (Table 44). Pregnant females were taken in all months except January and October and a lactating

TABLE 43.—*Reproductive data for* Liomys irroratus *based on information from throughout the range of the species. Mean and range are given for crown-rump length of embryos and length of testes when three or more values were available.*

Month of capture	Females: Number examined	Number pregnant	Number lactating	Crown-rump length of embryos	Males: Number examined	Length of testes
January	5	2	0	3,?	1	26
February	17	0	0		1	22
March	58	4	1	12.5(8-18)	0	
April	10	0	0		0	
May	18	1	1	8	0	
June	31	0	1		5	22.4(20-24)
July	40	4	4	11.0(6-15)	1	24
August	39	14	0	9.9(3-15)	11	20.5(13-25)
September	14	7	1	11.3(5-25)	5	17.2(7-20)
October	23	11	3	11.1(3-22)	2	15,20
November	19	7	1	14.3(8-20)	0	
December	7	1	0	24	3	20.0(15-23)

female was recorded in the latter month. Most of the pregnant females were taken in April, August, September, and November. No pregnant females have been recorded from 2 December to 5 February, although more than 70 females with reproductive data are available from that period. The mean number of embryos per female was 3.80 (mode three) with a range of two to six. Males with enlarged testes were taken in most months (Table 44), but males taken in November through February had testes that averaged much smaller than those of males taken between March and October.

Some data reported herein were recorded earlier by Hooper (1955:9) and Hall and Dalquest (1963:284). Wagner (1961:209) reported 17 females of *Liomys pictus* taken in the second half of March near Villa Flores, Chiapas, that carried the following number of embryos: one female with three embryos, 11 females with four embryos, four females with five embryos, and one female with six embryos. Eisenberg and Isaac (1963:65) and Eisenberg (1963*a*:11) found the mean of six litters of *L. pictus* born in captivity was 3.5 with a range of two to five. The gestation period for one of these litters was 24 days and for another 26 days (Eisenberg and Isaac, 1963:64; Eisenberg, 1963*a*:13). Immature individuals were found in each month for which Fleming (1969) had data (no specimens available for September, October, and December), excepting May. Immature specimens formed the largest proportion of the sample in March, 43.6 per cent being immature.

Liomys spectabilis.—Only one female of the six (one taken in March and five in September) with reproductive data contained embryos. This female, which was taken on 26 September at a place 2 2/10 mi. NE Contla, Jalisco, carried five

TABLE 44.—*Reproductive data for* Liomys pictus *based on information from throughout the range of the species. Mean and range are given for crown-rump length of embryos and length of testes when three or more values were available.*

	Females				Males	
Month of capture	Number examined	Number pregnant	Number lactating	Crown-rump length of embryos	Number examined	Length of testes
January	38	0	0		7	8.1(5-14)
February	38	3	0	15.7(10-25)	3	9.3(5-18)
March	20	2	0	6,7	9	16.3(5-24)
April	48	15	3	10.2(4-20)	0	
May	19	2	1	6,20	1	20
June	16	1	2	9	8	16.2(12-19)
July	15	1	0	?	10	18.9(6-27)
August	23	6	1	15.5(8-23)	11	19.5(10-25)
September	30	13	0	15.7(3-24)	27	17.9(4-25)
October	4	0	1		5	13.4(5-20)
November	14	5	1	13.4(5-20)	2	5,5
December	19	1	2	8	4	9.8(6-17)

embryos that measured 4 in crown-rump length. Four males trapped in mid-September had enlarged testes (those of two measuring 21 and the other two, 22).

Liomys salvini.—Reproductive data were known for 201 adult females of *Liomys salvini* of which 33 were pregnant (Table 45); no lactating females have been recorded. Females carrying embryos have been taken in eight different months (those available from April and June were nonpregnant and no data are available from September or October). Females with embryos formed the largest percentage of the total females in November, December, and February, although the total sample from the first two months was small. The mean number of embryos per female for this species was 3.55 (mode three) with a range of two to six. Adult males with enlarged testes have been taken in the months of January through April and in July and August (Table 45).

Goodwin (1946:375) reported that *Liomys salvini* in Costa Rica bred at all seasons of the year and the usual number in the litter was four. In El Salvador, Burt and Stirton (1961:54) recorded single females taken on 8 and 9 January, that each carried three embryos. and Felten (1957:154) reported a female taken in February with two embryos and one taken in March with three.

Liomys adspersus.—Fleming (1969, 1971) studied this species in the Panamá Canal Zone; he found the number of embryos ranged from two to four in five females, with a mean of 3.2. Fleming believed this spiny pocket mouse was a seasonal breeder, with females beginning to breed in late November, reaching a peak in March and April, and declining thereafter. Each female was found to produce an average of 1.44 litters per year. The male reproductive cycle was found to follow that of the female; testes of males were largest from October to April.

TABLE 45.—*Reproductive data for* Liomys salvini *based on information from throughout the range of the species. Mean and range are given for crown-rump length of embryos and length of testes when three or more values were available. No females were examined in which lactation was noted by the collector.*

	Females			Males	
Month of capture	Number examined	Number pregnant	Crown-rump length of embryos	Number examined	Length of testes
January	16	2	14,26	1	15
February	29	11	10.7(3-16)	6	15.7(7-19)
March	38	4	10.3(4-21)	15	15.1(4-25)
April	5	0		1	25
May	18	2	2,14	0	
June	19	0		2	7,9
July	41	9	9.4(3-20)	18	17.9(11-25)
August	28	2	7,4	6	15.2(11-19)
September	0			0	
October	0			0	
November	2	1	10	0	
December	5	2	12,24	0	

Heteromys desmarestianus.—A female from 2 mi. SW Santiago Sacatepéquez, Guatemala, taken on 1 February carried three embryos that measured 4 in crown-rump length and one from Finca El Paraíso, Chiapas, trapped on 21 March carried two embryos that measured 15. Males with enlarged testes were taken in Nicaragua in March (testes 17, 19) and June (testes 15, 20) and in Chiapas in June (testes 14, 18, 19, 19, 20, 20). Juveniles (deciduous premolars present) of *H. desmarestianus* are present in the Museum of Natural History from the months of January, February, June, July, and August.

Murie (1935:25) reported two females of *Heteromys desmarestianus* from British Honduras with four embryos each that were obtained on 25 February and 1 March, and a female from Guatemala that carried three embryos on 11 April. Kuns and Tashian (1954:101), in the course of a parasitological study in the vicinity of Palenque, Chiapas, obtained a female of *H. desmarestianus* on 21 July that contained three embryos. Goodwin (1934:30) reported the finding of a nest of this species near Puebla, Guatemala, that contained four young. Studying the ecology of mammals in the Panamá Canal Zone, Enders (1935:451) found a male with enlarged testes in January and a female taken at the same time that had been lactating recently. Fleming (1970:478), who also studied this species in the Panamá Canal Zone, recorded pregnant or lactating females in April, May, July, and November, and juvenile mice in January, February, July, August, October, and December. Based on his data, Fleming (1969, 1970:478) believed that *H. desmarestianus* breed at all times of the year in Panamá.

Heteromys gaumeri.—A female in the Museum of Natural History taken on 26 December 1962 at a place 7 km. N, 51 km. E Escárcega, Campeche, contained three embryos that measured 9 in crown-rump length. Eleven other females in the Kansas collection taken in January (1), March (1), July (7), and December (2) were nonpregnant. Males with enlarged testes were taken in March (19 in length), April (20), July (15, 16, 21), and August (17). Juveniles (deciduous premolars present) of *Heteromys gaumeri* were taken on the Yucatán Peninsula in January, April, July, and August.

Hatt (1938:336) recorded a female taken at Chichén Itzá, Yucatán, on 26 October that contained two embryos. Gaumer (1917:132) in his monograph on the mammals of Yucatán stated females of *H. gaumeri* gave birth to four young.

Heteromys goldmani.—Wagner (1961:209) believed that this species bred from May to December in the vicinity of Villa Flores, Chiapas, and produced three or four embryos.

Heteromys lepturus.—At Vista Hermosa, Oaxaca, on 28 June a female was taken that carried two embryos, which measured 7 in crown-rump length; a lactating female was taken at this place on the following day. Four males taken in the vicinity of Vista Hermosa in late June had testes that measured 8, 13, 20, and 22 in length. Also a juvenile was taken at this same time.

Heteromys anomalus.—Rood (1963:189) reported that two wild-caught females from Venezuela gave birth to young on 2 April (one young) and 17 May (three young). He found that a majority of females trapped at Rancho Grande, Venezuela, in April and May were either lactating or pregnant, whereas those caught in March were not. However, Rood opined that some breeding occurred in winter because immature individuals, probably less than two months old, were taken in April. Rood and Test (1968:94) found no males of *H. anomalus* with completely retracted testes in the period 24 April to 30 May, although some testes were regressing toward the end of this period.

Heteromys australis.—The only reproductive data that I have available for this species are the presence of juvenile specimens in the Darién of Panamá on 6 June, 27 June, and 19 July.

Heteromys oresterus.—Goodwin (1946:373) in his report on Costa Rican mammals stated that *Heteromys oresterus* produced from three to five young per litter with four being the usual number.

Conclusions.—The results of pairwise comparisons of the embryo counts for four species of *Liomys* (*L. spectabilis* not included) and *Heteromys desmarestianus* are given in Table 46. *Liomys irroratus* was found to have a significantly higher number of embryos per litter than the other four species (three *Liomys* and one *Heteromys*). The number of embryos found in specimens of *Liomys pictus* was significantly more than in *Heteromys desmarestianus.* The count for *pictus* probably will be found to be significantly higher than in specimens of *adspersus* when more data are available for the latter species. There was no significant difference between *pictus* and *salvini,* although *pictus* average a slightly higher embryo count. No significant difference was found between the embryo counts of *Liomys salvini, Liomys adspersus,* and *Heteromys desmarestianus.* Whether the difference in embryo counts between these species is a reflection of interspecific genetic difference or some ecological difference cannot be stated at the present time.

TABLE 46.—*Pairwise comparisons of embryo counts for four species of* Liomys *and one of* Heteromys *using Wilcoxon two-sample test (Sokal and Rohlf, 1969:392-394).*

	Liomys irroratus	*Liomys pictus*	*Liomys salvini*	*Liomys adspersus*	*Heteromys desmarestianus*
Liomys irroratus (52)	4.39				
Liomys pictus (49)	*	3.80			
Liomys salvini (33)	***	ns	3.55		
Liomys adspersus (5)	*	ns	ns	3.20	
Heteromys desmarestianus (7)	*	**	ns	ns	3.28

From the available data, *Liomys irroratus* and *Liomys salvini* breed throughout the year. *L. pictus* appears to reproduce at most times of the year, although reproductive activity seems to be at a low level or to have ceased in the period from mid-December through January (see Fleming, 1971:67). Fleming (1970:478) believed *Heteromys desmarestianus* bred at all times of the year in Panama. The only species for which extensive data are available that appears to be a seasonal breeder is *Liomys adspersus* in which Fleming (1969, 1971:65-69) found pregnant or lactating females only in the period from December through May. Wagner (1961:209) has suggested that *Heteromys goldmani* may breed only from May through December, but he supplied no supportive data. Why one species of *Liomys* should be a seasonal breeder while the other species of the genus and *Heteromys desmarestianus* have some individuals breeding at most seasons of the year is not readily apparent at the present time. It should be pointed out that these comments are based on data for the species from throughout their geographic ranges, which is the best that can be done at the present time. However, when more data become available, geographic variation and variation from one year to another may be expected in the timing of the reproductive season within a species.

PTERYGOID STRUCTURE

The shape of the pterygoid bones of specimens of *Liomys irroratus* differs from that of all other species studied (Fig. 61). In *Liomys* and *Heteromys* the pterygoid bones extend ventrally and then turn laterally. However, in specimens of *Liomys irroratus* the bone extends laterally noticeably farther than in other species, giving the pterygoids a teardrop shape when viewed ventrally. In all other species this lateral expansion is minor and the bone is straight in appearance when viewed ventrally. Specimens of *Liomys adspersus* probably have the broadest pterygoids of the remaining four species of *Liomys*, and some specimens of *Heteromys* have the tips of the bones expanded, but both are distinguishable from *irroratus*. Shape of the pterygoids has proven to be a useful

FIG. 61.—Pterygoid structure of five species of *Liomys* and one of *Heteromys* illustrating the breadth of the wings of the pterygoids and the shape of the interpterygoid fossa. The species are as follows: A, *Liomys irroratus* (KU 38373); B, *Liomys pictus* (KU 96067); C, *Liomys spectabilis* (KU 96045); D, *Liomys salvini* (KU 68847); E, *Liomys adspersus* (KU 121538); F, *Heteromys desmarestianus* (KU 95036). The scale at the right is three millimeters long.

characteristic for separating cleaned crania of *Liomys irroratus* from crania of *Liomys pictus* in areas of potential sympatry between the species.

The shape of the interpterygoid fossa is rather variable within the species of *Liomys*; however, in all it is somewhat U-shaped anteriorly (Fig. 61). In specimens of *Heteromys*, on the other hand, the interpterygoid fossa narrows anteriorly into an acute point, giving the fossa a V-shape (see also Goldman, 1911:15).

PELAGE

Variation in the coloration of the middorsal pelage was analyzed with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment (see Bowers, 1956; Selander *et al.*, 1964; Johnston, 1966; Selander and Johnston, 1967, for discussion of colorimetric techniques). Flatness of the 100 per cent line was maintained within limits of 0.5 per cent peak-to-peak, and flatness of the 0 line within limits of 0.25 per cent. Wavelength accuracy of the Spectronic 505 is 0.5 millimicrons, and repeatability, 0.2 millimicrons. White standards of 100 per cent reflectance were prepared from magnesium sulfate.

From curves of percentage reflectance in the range of wavelengths from 400 to 700 millimicrons, trichromatic coefficients (x, y, z) were derived by the 10 selected ordinate method, which involves a total of 30 readings from each curve. This was done using the trichromatic coefficient computing chart for Illuminant C produced by Bausch and Lomb (catalog no. 33-28-13). From the trichromatic coefficients, the psycho-physical descriptions of the colors were computed in terms of brightness (in per cent), dominant wavelength, and per cent excitation purity (see Judd, 1933). Brightness is simply the comparison of the sum of all the wavelength reflectances with the sum of those reflectances from the standard block and expressed as the per cent of the standard reflectance. Dominant wavelength refers to the hue of the sample and purity refers to the percentage of pure color reflected by the sample. The conversion of the trichromatic coefficients to the psycho-physical descriptions was done with the use of a computer program written in Fortran IV by S. A. Rohwer at The University of Kansas.

Specimens used for color determination were carefully selected whenever possible so as to represent total variation in the species taxonomically, ecologically,

TABLE 47.—*Dorsal color of five species of* Liomys *and two of* Heteromys. *Statistics given are mean, two standard errors of the mean, and range.*

Species	N	Brightness	Dominant wavelength	Purity
Liomys irroratus	10	9.36 ± 1.036 (7.50-11.60)	583.0 ± 1.34 (579.5-587.1)	20.86 ± 2.366 (13.58-25.31)
Liomys pictus	10	9.57 ± 0.834 (7.25-11.25)	583.3 ± 0.50 (582.1-584.3)	26.37 ± 3.686 (15.06-32.32)
Liomys spectabilis	10	8.54 ± 0.514 (7.60-10.30)	583.8 ± 1.22 (581.8-588.5)	27.69 ± 30.32 (15.58-34.44)
Liomys salvini	10	7.58 ± 1.032 (5.20-11.20)	582.9 ± 1.10 (580.4-585.0)	20.58 ± 1.798 (15.49-24.46)
Liomys adspersus	5	7.86 ± 0.720 (6.55-8.55)	581.6 ± 1.65 (579.4-583.2)	21.12 ± 2.090 (18.18-24.40)
Heteromys desmarestianus	10	6.56 ± 0.322 (5.75-7.35)	584.3 ± 1.48 (580.4-585.3)	20.40 ± 2.280 (15.38-28.40)
Heteromys gaumeri	5	8.21 ± 0.302 (7.65-8.55)	582.5 ± 1.16 (581.5-584.3)	23.47 ± 4.156 (19.48-29.09)

and geographically. Therefore, values for each species in Table 47 should fairly closely represent the range of variation for the species as a whole.

Coloration of dorsum.—The dominant wavelength or hue of the dorsal pelage did not differ to any great extent among the seven species tested. Specimens of *Heteromys desmarestianus*, with an average dominant wavelength of 584.3 millimicrons, revealed the most redness and specimens of *Liomys adspersus*, with an average dominant wavelength of 581.6 millimicrons, showed the least. The means for the remaining five species fell between 582.5 and 583.8 millimicrons and, considering the total range of variation for all species, there appear to be no significant differences based on dominant wavelength.

However, specimens of *Liomys pictus* and *Liomys spectabilis* exhibited a much higher per cent purity than the other species, having mean values of 26.37 and 27.69, respectively. The per cent purity for specimens of *Heteromys gaumeri* with a mean value of 23.47 fell between those taxa with high values and the remaining four species with mean values ranging from 20.40 and 21.12. Specimens of *Liomys pictus* and *Liomys irroratus* were the palest of those tested (mean per cent brightness values 9.57 and 9.36, respectively). Specimens of *Heteromys gaumeri* and *Liomys spectabilis* had nearly the same mean per cent brightness (8.21 and 8.54, respectively) as was true for specimens of *L. salvini* and *L. adspersus* (7.58 and 7.86, respectively). Specimens of *Heteromys desmarestianus* with a mean per cent brightness of 6.56 were the darkest of the seven species under consideration.

Typical Ridgway (1912) color designation for the overall dorsal coloration of these seven species are as follows: between Chaetura Drab and Clove Brown (*Liomys irroratus*); Dresden Brown to Mummy Brown (*Liomys pictus* and *Liomys spectabilis*); Clove Brown to Dark Olive (*Liomys salvini* and *Liomys adspersus*); near Raw Umber (*Heteromys desmarestianus*); Saccardo's Umber to Sepia (*Heteromys gaumeri*).

Characteristics.—A lateral stripe separating the dorsal coloration from the white belly pelage is absent in specimens of *Liomys salvini* and *Liomys adspersus.* In the other three species of *Liomys* (*irroratus, pictus, spectabilis*) and two species of *Heteromys* (*desmarestianus* and *gaumeri*) that I have examined, there is in nearly all specimens a stripe of differently colored pelage that separates the dorsal coloration from that of the venter, although the stripe may vary in color and width. In specimens of *Liomys irroratus,* the lateral stripe is generally a buffy to a pale pinkish color and usually is relatively narrow (in some specimens of *L. i. torridus* it may be absent). Never is the stripe in *irroratus* as strikingly noticeable as the ochraceous lateral stripe found in specimens of *Liomys pictus* and *Liomys spectabilis.* The lateral stripe in specimens of *Heteromys gaumeri* is much the same color as in *pictus* and *spectabilis,* but in some specimens the stripe is noticeably broad, unmatched in any of the other species under consideration, whereas in other specimens the stripe is as narrow as in *pictus* or *spectabilis.* Specimens of *Heteromys desmarestianus* have a narrow buffy lateral stripe that is generally faint.

On specimens of *Liomys salvini* and *Liomys adspersus,* the terminal one-third to one-half of each slender dorsal hair is curved upward so that it stands out conspicuously beyond the spines. A museum study skin of one of these species when viewed laterally has a fuzzy appearance. This characteristic is not seen in the other three species of *Liomys* or in *Heteromys desmarestianus* and *H. gaumeri.* Specimens examined for pelage coloration and characteristics are listed below.

Liomys irroratus.—San Gregorio Altapulco, Distrito Federal, 1 (KU 28052); 5½ km. N Agua del Obispo, Guerrero, 1 (KU 99783); Omilteme, Guerrero, 1 (KU 98761); 2.6 mi. E Etzatlán, Jalisco, 1 (KU 96019); 1½ mi. N Zaragoza, Nuevo León, 1 (KU 98635); 4 mi. ESE Oaxaca, Oaxaca, 1 (KU 62633); 1 mi. SSW Tilapa, Puebla, 1 (KU 62623); 10 mi. NE San Luis Potosí, San Luis Potosí, 1 (KU 39898); Soto la Marina, Tamaulipas, 1 (KU 55880); 4 km. W Tlapacoyan, Veracruz, 1 (KU 24010).

Liomys pictus.—Los Sabinos, Guerrero, 1 (KU 28458); 0.9 mi. NE Contla, Jalisco, 1 (KU 96033); San Sebastián, Jalisco, 1 (KU 112277); 7.3 mi. ESE Amatlán de Cañas, Nayarit, 1 (KU 98942); 10 mi. S Juchatengo, Oaxaca, 1 (KU 98775); 20 mi. S, 5 mi. E Sola de Vega, Oaxaca, 1 (KU 98768); 10 mi. W, 2 mi. N Tehuantepec, Oaxaca, 1 (KU 54698); 5 mi. NW Mazatlán, Sinaloa, 1 (KU 85792); Alamos, 54 km. E Navajoa, Sonora, 1 (KU 89461); Puente Nacional, Veracruz, 1 (KU 19371).

Liomys spectabilis.—8 km. N Contla, Jalisco, 3 (KU 96035-37); 3.3 mi. NE Contla, Jalisco, 4 (KU 96042-45); 2.2 mi. NE Contla, Jalisco, 3 (KU 96050-52).

Liomys salvini.—22 km. S San José, Costa Rica, 1 (KU 39252); 1 mi. NW San Salvador, El Salvador, 1 (KU 71079); 3 mi. E Jocotán, Guatemala, 1 (KU 84125); 1 mi. SE Monogoy, Guatemala, 1 (KU 71068); 16 km. SW Tapachula, Chiapas, 1 (KU 120602); 6 mi. NW Tonalá, Chiapas, 1 (KU 68839); Hda. Bellavista, Nicaragua, 1 (KU 106378); La Danta, 1 km. E Esquipulas, Nicaragua, 1 (KU 115352); 4 mi. W Managua, Nicaragua, 1 (KU 71139); Santa Rosa, 17 km. N, 15 km. E Boaco, Nicaragua, 1 (KU 110403).

Liomys adspersus.—2 km. NE Buenos Aires, Panamá, 4 (KU 121527-30); Las Cumbres, 7 km. N, 2 km. W Pueblo Nuevo, Panamá, 1 (KU 121535).

Heteromys desmarestianus.—1 mi. SW Santiago Sacatepéquez, Guatemala, 1 (KU 71256); 2 mi. SW Santiago Sacatepéquez, Guatemala, 1 (KU 71247); Finca El Paraíso, Chiapas, 1 (KU 66583); 8 mi. (by road) NW Pueblo Nuevo, Chiapas, 1 (KU 95034); 7.5 mi. (by road) NW Pueblo Nuevo, Chiapas, 2 (KU 95037-38); Sabana de Quintín, Chiapas, 1 (KU 102653); 2 km. N, 6 km. E Esquipulas, Nicaragua, 2 (KU 115410-11); Santa María de Ostuma, Nicaragua, 1 (KU 106523).

Heteromys gaumeri.—3 km. N Pisté, Yucatán, 3 (KU 92123-24, 92128); 2 km. N Pisté, Yucatán, 1 (KU 92130); Pisté, Yucatán, 1 (KU 92133).

Distribution

Although the distribution and ecology of the various species of *Liomys* were discussed in the systematic accounts, I have drawn this information together here for comparative purposes. Only a brief summary of the information from the systematic accounts is given below.

Liomys irroratus.—This species occurs on the Mexican Plateau and adjacent areas, from southern Texas and Chihuahua in the north to the Sierra Madre del Sur of Oaxaca in the south. The vegetation in the areas where *irroratus* occurs is mainly steppe, thicket, and scrub desert and montane formation series (Wagner, 1964:223); the montane formation series contains xerophytic plants, mainly pine and oak. *Liomys irroratus* occurs sympatrically only with *Liomys pictus,* although it approaches the range of *Liomys spectabilis.* In those areas where *irroratus* and *pictus* are sympatric, which is in a band from central Jalisco to the mountains of the Sierra Madre del Sur of Oaxaca, *irroratus* is generally found in the drier areas and *pictus* in the moister areas. Generally, therefore, they are microallopatric in these areas.

Liomys pictus.—This species is known along the western coast of México from Sonora to northwestern Chiapas, in the central valley of Chiapas, and in southern Veracruz. *Liomys pictus* occurs most often in seasonal formation series type of vegetation, mainly lowland dry forest, although some specimens are known from the xerophytic montane formation (Wagner, 1964). *Liomys pictus* occurs sympatrically with *Liomys irroratus* (see above), *Liomys salvini* (see below), and *Liomys spectabilis* (see below).

Liomys spectabilis.—This species is known only from the relatively moist interior basins of southeastern Jalisco. Because the area has been significantly altered by agricultural practices, it is difficult to determine the exact habitat occupied by the species. At three locations *pictus* and *spectabilis* were obtained in the same trapline in such habitats as the edge of a cornfield and around clumps of brush in a heavily grazed pasture.

Liomys salvini.—Occurring along the Pacific coast and adjacent mountains of Central America from southeastern Oaxaca to central Costa Rica, *L. salvini* also is known from dry river valleys of the Caribbean drainage such as along the Río Motagua in Guatemala. Vegetation of these areas is generally lowland dry forest and lower montane dry forest, which is largely pine-oak (Stuart, 1966).

This species is known to occur sympatrically with *Liomys pictus*, the area of sympatry being in southeastern Oaxaca and northwestern Chiapas. No data are available concerning the ecological condition under which the two species have been taken in the area of sympatry, but males of the two species do show character displacement there.

Liomys adspersus.—This geographically restricted species is known only from Pacific lowlands of central Panamá and the headwaters of the Caribbean drainage in the vicinity of the Panamá Canal; this is an area of savanna. The nearest species geographically and phylogenetically is *L. salvini*, which occurs as far south as central Costa Rica, but the two species are separated by the lowland rainforest occurring around the Golfo Dulce of Costa Rica and western Panamá.

Heteromys.—Most of the species of *Heteromys* (except *gaumeri*) occurring in México and Central America inhabit areas of lowland rainforest and quasi-rainforest, lower montane wet forest and cloud forest, and to some extent the lower montane dry forest (Stuart, 1966). However, even in the latter areas they are found in very mesic situations. At only a few places have *Heteromys* and *Liomys* been taken together (Hda. Tepeyac, Nicaragua, for example); when more precise data are available, it likely will be found that microallopatry is the case (even at Hda. Tepeyac), as in the vicinity of Esquipulas, Nicaragua, where *H. desmarestianus* occurs in the cooler, moister uplands and *Liomys salvini* in the hotter, drier lowlands. The one exception to *Heteromys* occurring in mesic situations is *H. gaumeri*, which occurs in lowland dry forest and thorn forest on the Yucatán Peninsula (Stuart, 1966) in the absence of *Liomys*.

OTHER STUDIES

Several studies by other researchers have dealt with *Liomys* and *Heteromys* and should be mentioned; these could not be used for analysis of relationships, however, because some species were not included. Eisenberg (1963*a*, 1963*b*, 1967) has presented some interesting studies on the behavior of heteromyid rodents, which included *Liomys pictus*, *Heteromys anomalus*, *H. desmarestianus*, and *H. lepturus*. Behavioral studies such as these and other types such as huddling experiments certainly would be useful in understanding the relationships of members of the genera *Liomys* and *Heteromys*, especially in areas of actual or potential sympatry. Two studies of anatomy, one by Hatt (1932) on post-cranial skeletal anatomy and the other by Quay (1965) on sebaceous and suboriferous glands, have included comments on some species of *Liomys* and *Heteromys*. The study by Hudson and Rummel (1966) on water metabolism and temperature regulation of *Liomys salvini* and *Liomys irroratus* is the only physiological work on members of the genus of which I am aware.

A great deal still remains to be learned about the biology and systematics of species of *Liomys* and *Heteromys*. One important aspect of the biology of these animals has been virtually unstudied—their ecology, where only the work of Fleming on *Liomys adspersus* is the exception. Good autecological studies of any other species would be of real value, but of even more interest would be studies of species in areas of actual or potential sympatry. Three areas in which the ecological relationships of *Liomys irroratus* and *L. pictus* could be successfully studied are in 1) central Jalisco in the vicinity of Guadalajara; 2) to the north of Iguala, Guerrero, southward through the Balsas basin to Chilpancingo and on to Acapulco; and 3) southward from Sola de Vega, Oaxaca, over the Sierra Madre del Sur to Puerto Angel. The ecological relationships of *Liomys pictus* to *L. salvini* would need to be studied in the area from Reforma, Oaxaca, to Tonalá, Chiapas. The ecological preferences of members of genus *Liomys* could be compared with those of *Heteromys* in a place such as Esquipulas, Nicaragua, where *salvini* occurs at lower elevations and *desmarestianus* at higher elevations. Studies of ecological physiology would be extremely useful in understanding habitat preferences of the species.

More systematic work in such areas as serology and immunology still remains to be done. A much more extensive survey of karyological differences among the species will need to be done before these characteristics can be fully understood. Many anatomical systems, such as muscular and gastric, have not been studied.

It is my hope that the present study has resulted in a workable systematic arrangement of members of the genus *Liomys* so that studies such as those described above can be carried out in a more meaningful way.

EVOLUTIONARY AND ZOOGEOGRAPHIC RELATIONSHIPS

Removal of *"Liomys" centralis* from the genus limits the known fossil material of *Liomys* to late Pleistocene and sub-Recent cave deposits, thereby eliminating the possibility of deducing evolutionary relationships within the genus based upon the paleontological record. Therefore, in order to obtain an objective estimate of the evolutionary relationship among the five species of *Liomys* and their relationship with *Heteromys* (characters used in this analysis based upon *desmarestianus, gaumeri,* and *lepturus* but mainly the first), I have employed cluster analyses based upon both correlation and distance matrices and a principal components analysis, both of which are part of the NT-SYS programs, and a Prim Network. Characters used for analysis and methods for scoring them are given in Appendices III and IV, respectively; these are mainly characteristics analyzed and discussed in the previous section. These characters were used in the NT-SYS programs to obtain a representation of the phenetic relationships of the species. The Prim Network gives an estimation of the cladistic and patristic centers for the group of OTU's (species) being analyzed and thereby provides a useful and objective framework for inference of primitive character states.

Fifty-three characters were contained in the original matrix for analyses (see Appendix III). However, those characteristics dealing with ectoparasite faunas and morphology of spermatozoa had to be eliminated because data were not available for all species being analyzed. The remaining characteristics were submitted to a character correlation analysis and those characters found to be highly correlated with others in the matrix were eliminated. Most characters eliminated appeared to be measures of size (the only measure of general size remaining in the matrix is greatest length of skull). The final matrix used in all analyses in this section, therefore, contained only 30 characters (marked by an asterisk in Appendix III).

Examination of the correlation matrix (Table 48) and correlation phenogram (Fig. 62) based upon this matrix (coefficient of cophenetic correlation is 0.955) reveals that *Liomys pictus* and *Liomys spectabilis* are the most highly correlated species. The next most highly correlated pair of species and the only other pair that possesses a positive correlation coefficient is *Liomys salvini* and *Liomys adspersus. Liomys irroratus* exhibits only negative correlation coefficients with the other five species included in the analysis; based upon these values it appears that *irroratus* is only slightly closer to *L. pictus* and *L. salvini* than to *Heteromys.* The characteristics of *irroratus* show less correlation with those of *spectabilis* than with these three taxa and the least correlation with those of *adspersus. Heteromys* is relatively far removed from species of *Liomys* in the matrix, being closest to *L. irroratus* and farthest from *L. pictus*; it is grouped with *irroratus* in the phenogram, but it must be remembered that they are negatively correlated. *Liomys pictus* and *L. spectabilis* show little correlation with *L. salvini* and *L. adspersus* with all correlation coefficients between the species being over a −0.3.

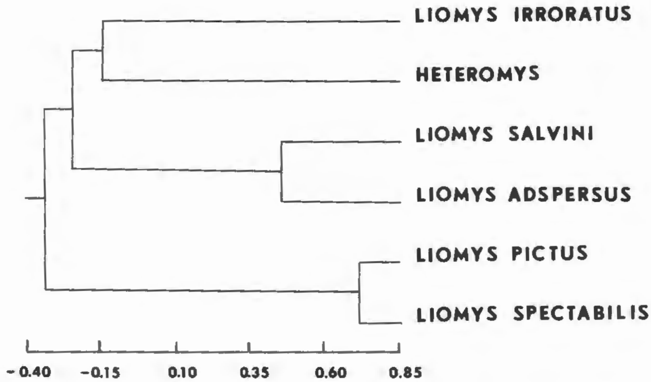
The distance matrix (Table 48) and distance phenogram (Fig. 62) based upon this matrix (coefficient of cophenetic correlation 0.985) reveal nearly the same pattern as their correlation counterparts. In the phenogram, the five species of

TABLE 48.—*Correlation and distance matrices based upon 30 characters comparing the five species of* Liomys *and a composite of three species of* Heteromys, *mostly* desmarestianus.

	Liomys irroratus	*Liomys pictus*	*Liomys spectabilis*	*Liomys salvini*	*Liomys adspersus*	*Heteromys* species
Liomys irroratus	1.000					
Liomys pictus	−0.119	1.000				
Liomys spectabilis	−0.220	0.713	1.000			
Liomys salvini	−0.115	−0.350	−0.432	1.000		
Liomys adspersus	−0.301	−0.335	−0.363	0.442	1.000	
Heteromys sp.	−0.152	−0.525	−0.404	−0.307	−0.295	1.000
Liomys irroratus	0.000					
Liomys pictus	1.187	0.000				
Liomys spectabilis	1.257	0.594	0.000			
Liomys salvini	1.160	1.249	1.306	0.000		
Liomys adspersus	1.348	1.335	1.367	0.855	0.000	
Heteromys sp.	1.679	1.864	1.812	1.740	1.800	0.000

Liomys form a cluster separate from *Heteromys*; examination of the distance matrix reveals that all species of *Liomys* are approximately equidistant from *Heteromys*, with *Liomys irroratus* being phenetically the closest with a distance coefficient of 1.679 and *Liomys pictus* being the most distant with a coefficient of 1.864. Within the species of *Liomys* on the phenogram, *L. salvini* and *L. adspersus* form a cluster as do *L. pictus* and *L. spectabilis*, whereas *L. irroratus* forms a cluster by itself. From the phenogram, it appears that *irroratus* is slightly closer to the *pictus-spectabilis* group than the *salvini-adspersus* group; however, values in the matrix show *salvini* to be closest to *irroratus*, but only slightly more so than *pictus*. *L. spectabilis* is more distant from *irroratus* than the latter two species and *adspersus* is the most distant of all the species within the genus. The *pictus-spectabilis* group and *salvini-adspersus* group are phenetically distant from each other with the lowest distant coefficient between the members being 1.249. The lowest phenetic distance coefficient between a pair of species is 0.594 between *pictus* and *spectabilis* and the next lowest is 0.855 between *salvini* and *adspersus*.

In the principal components analysis, 100 per cent of the phenetic variation based upon the matrix of correlation among the 30 characters was explained by the first five components as follows: component I, 44.79; component II, 28.75; component III, 16.47; component IV, 6.65; component V, 3.34. Results of the factor analysis are given in Table 49 and two-dimensional plots of component I against components II to V are given in Fig. 63. Along the first principal component *Heteromys* is widely separated from the five species of *Liomys* and characters with high weighting in this component are those that tend to distinguish the two genera. Among the highly weighted characters were: 19, presence or absence of accessory enamel islands on the molars (positive value); 20, number



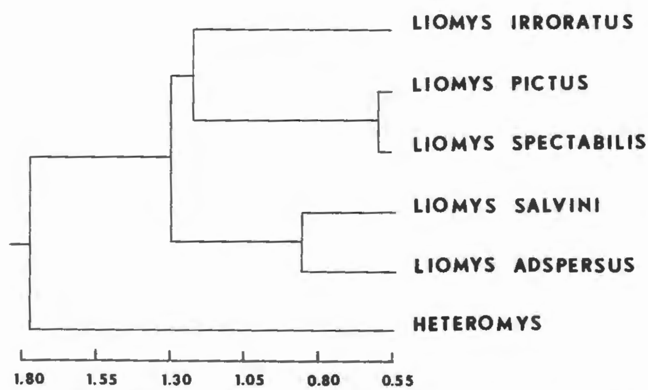


FIG. 62.—Correlation (upper) and distance (lower) phenograms for five species of *Liomys* and a composite of values for *Heteromys* computed from correlation and distance matrices, respectively, based on standardized characters and clustered by unweighted pair-group method using arithmetic averages. The cophenetic correlation coefficient of the correlation phenogram is 0.955 and for the distance phenogram is 0.985.

of lophids on the lower premolars (negative); 22, position of entostyle on upper premolar (negative); 34, length of baculum divided by length of hind foot times 100 (positive); 45, shape of interpterygoid fossa (negative); 47, soles of hind feet (negative); and 49, ecological relationships (negative). Other characters receiving relatively high values but not as high as the previous set were: 1, greatest length of skull (negative); 14, condition of the posterior margin of the interparietal bone (negative); 23, length of P4 divided by greatest length of skull times 100 (positive); 30, length of glans divided by length of baculum times 100 (negative); 32, morphology of baculum (positive); and 52, per cent brightness of dorsal pelage (positive). It should be noted that along this component, which tends to separate

TABLE 49.—*Factor matrix from correlation among 30 characters of the five species of* Liomys *and a composite of three species of* Heteromys, *mostly* desmarestianus.

Character	Component I	Component II	Component III	Component IV	Component V
1	−0.731	0.020	0.230	0.586	0.265
14	−0.701	0.510	−0.142	−0.450	0.157
15	0.497	−0.353	−0.377	0.362	−0.596
16	−0.688	−0.428	0.046	0.584	0.012
17	−0.418	0.665	0.357	−0.060	−0.502
18	0.665	−0.735	0.095	−0.082	0.049
19	0.969	−0.177	−0.165	0.020	0.054
20	−0.969	0.177	0.165	−0.020	−0.054
21	0.665	−0.735	0.095	−0.082	0.049
22	−0.840	−0.542	−0.018	−0.028	−0.004
23	0.745	0.153	−0.616	−0.074	0.190
27	0.542	−0.635	0.521	−0.179	0.008
28	−0.204	0.931	−0.269	0.136	−0.028
30	−0.733	−0.239	−0.623	−0.131	−0.017
31	0.341	0.874	0.241	0.246	−0.031
32	0.731	0.343	0.576	−0.124	−0.033
33	0.094	0.155	0.639	0.688	0.293
34	0.943	0.189	0.268	0.013	0.059
35	−0.679	−0.513	−0.515	0.096	0.038
36	−0.419	−0.758	0.442	−0.223	−0.070
37	−0.531	−0.763	−0.364	0.040	0.042
45	−0.969	0.177	0.165	−0.020	−0.054
46	−0.039	−0.036	0.966	−0.242	−0.073
47	−0.969	0.177	0.165	−0.020	−0.054
48	0.422	0.481	−0.739	−0.068	0.201
49	−0.969	0.177	0.165	−0.020	−0.054
50	−0.204	0.931	−0.269	0.136	−0.028
51	−0.489	0.767	0.003	−0.392	0.137
52	0.748	0.380	−0.431	0.198	−0.268
53	0.568	0.735	0.361	0.015	0.084

the two genera, *Liomys irroratus*, although far removed from *Heteromys*, is the species nearest to it and that *Liomys pictus* is farthest from *Heteromys*.

The second principal component, which accounts for more than a quarter of the total phenetic variation, appears to distinguish the species groups within the genus *Liomys*. The three characters with the highest loading (all positive) in this component were 28 (number of lobes on urethral lappets), 31 (length of tip of glans penis divided by total length of glans times 100), and 50 (presence or absence of lateral stripe). Other characters with relatively high positive loading in

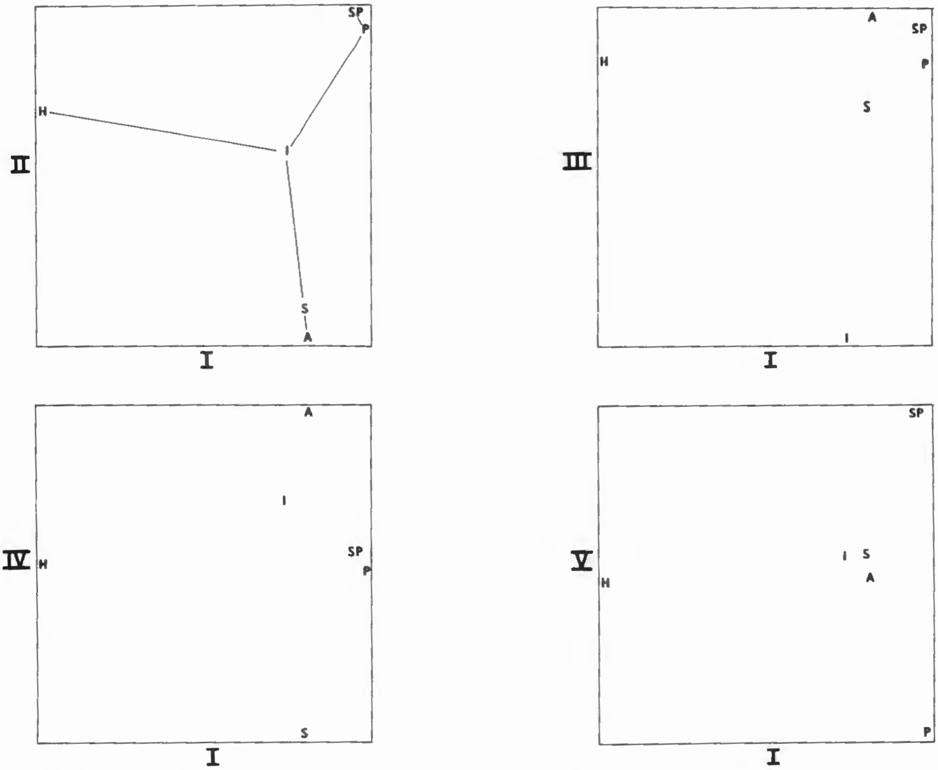


FIG. 63.—Two-dimensional projections of the first five principal components illustrating the phenetic position of the five species of *Liomys* and a composite of values for *Heteromys*. Superimposed upon the projection of component I plotted against component II is the least interconnected network based upon the distance matrix. Symbols used are as follows: A, *Liomys adspersus*; H, *Heteromys*; I, *Liomys irroratus*; P, *Liomys pictus*; S, *Liomys salvini*; SP, *Liomys spectabilis*.

this component were 51 (dominant wavelength of dorsal coloration) and 53 (per cent purity of dorsal coloration). Characters with high negative values in this component were 18 (wear pattern of molars), 21 (re-entrant angle on labial margin of metalophid), 36 (fundamental number of chromosomes), and 37 (type of X-chromosome). In this component, *Liomys pictus* and *Liomys spectabilis* form a group at the top of the plot and *Liomys salvini* and *Liomys adspersus* form another group at the bottom of the plot. *Liomys irroratus* occupies an intermediate position between these two groups. It should be noted that although *Heteromys* is widely separated from *irroratus* in the first component, it is near that species in the second component.

Superimposed upon the plot of component I against II (Fig. 63) is the least interconnected network of species based upon the distance matrix. The network shows *Heteromys* connected only to *Liomys irroratus*. *Liomys irroratus*, aside from being connected with *Heteromys*, also is connected with *Liomys pictus* and

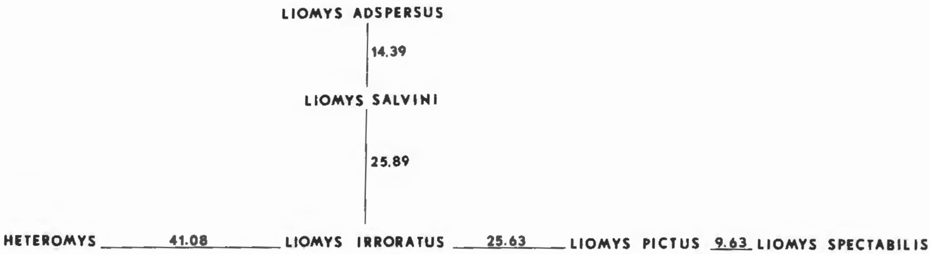


FIG. 64.—A Prim Network illustrating relationships between the five species of *Liomys* and a composite of values for *Heteromys*. Characters used and methods for scoring them are given in appendices III and IV, respectively.

Liomys salvini. L. pictus in turn is connected with *Liomys spectabilis* and *L. salvini* with *L. adspersus.*

In the third component, which accounts for slightly more than 15 per cent of the total phenetic variation, the characters with the high loading were those that distinguished *L. irroratus* from the other species, especially of *Liomys.* Characters with high positive loading were 27 (amount of sculpturing on glans penis), 32 (morphology of baculum), 33 (length of baculum), and 46 (number of plantar tubercles); characters with high negative loading were 23 (length of P4 divided by greatest length of skull times 100), 30 (length of glans divided by length of baculum times 100), 35 (number of chromosomes), and 48 (reproductive rate). Characters 46 and 48 had the highest loading values. In component III, *Liomys salvini* is the species nearest to *irroratus*, which is located at the bottom of the plot, and *Liomys adspersus* is the species farthest from *irroratus.*

The fourth component, which accounts for less than seven per cent of the total phenetic variation, is evidently heavily influenced by those characters that distinguish *Liomys salvini* and *Liomys adspersus*, which are located at opposite edges of the plot with the other species located near the center. Characters with high positive loading in this component were 1 (greatest length of skull), 16 (shape of termination of nasal bones), 31 (length of tip of glans penis divided by length of glans times 100), and 33 (length of baculum), whereas 14 (condition of posterior margin of interparietal bone), 36 (fundamental number of chromosomes), 46 (number of plantar tubercles), and 51 (dominant wavelength of dorsal coloration) had high negative values. Generally for factor component IV and V loading values were much lower than for the first three components.

The fifth component, which accounts for less than four per cent of the total phenetic variation, is generally influenced by those characters that distinguish *Liomys pictus* and *Liomys spectabilis*, which are located at opposite edges of the plot with the other species clustered near the middle. Characters with high positive values for this component were 1 (greatest length of skull), 33 (length of baculum), and 48 (reproductive rate) and those with the highest negative values were 15 (division of interparietal), 17 (length of nasals in comparison with premaxillaries), and 52 (per cent brightness of dorsal coloration).

The Prim Network shows *Liomys irroratus* at the cladistic and patristic center of the six species under study (Fig. 64). It seems plausible (see also below) that *L. irroratus* occupies such a position within the genus *Liomys* and that the other members of the genus were derived from a stock similar to it. However, based upon study of the paleontological record presented by Wood (1931, 1935), there may have been separate origins of the genera *Liomys* and *Heteromys* from the early heteromyine stock (*Peridiomys-Proheteromys* complex). This would mean that on the Prim Network the cladistic and patristic centers for the two genera would lie somewhere between *Liomys irroratus* and the representatives of *Heteromys* studied.

If *Liomys irroratus* is the living species most nearly resembling the ancestral form of the genus, it would be expected to share more characters with the "sister-group" *Heteromys* than would other *Liomys*; characters shared between the genera can be presumed to have probably been present in their common ancestor. *Liomys irroratus* and *Heteromys lepturus* exhibit similarities in the structure of the glans penis such as the amount of sculpturing, number of urethral lappets, ratio of length of glans to length of baculum, and amount of tip of glans that is exposed. The morphology of the baculum of *Liomys irroratus* and *Heteromys desmarestianus* and *H. gaumeri* is nearly identical. Both *L. irroratus* and *H. desmarestianus* have a chromosome number of 60 and a large submetacentric X-chromosome (the latter is also true of *L. adspersus* and *L. salvini*). A lateral stripe is present in most specimens of *L. irroratus* and *H. desmarestianus* as well as *Liomys pictus* and *Liomys spectabilis.* It seems most likely to me (in view of what is known about *Perognathus*) that the spermatozoa of *Heteromys* will be found to be similar to those of *irroratus, pictus,* and *spectabilis* and unlike those of *salvini* and *adspersus.* The upper premolar of *Liomys salvini* and *Liomys adspersus* more closely resembles those of *Heteromys* than do other species of *Liomys,* but some differences also were noted. These two species of *Liomys* have a high fundamental number, which is near the value for *Heteromys desmarestianus.* The anopluran louse, *Fahrenholzia fairchildi,* has been reported from *L. salvini, L. adspersus,* and *H. desmarestianus,* but it seems probable to me that this louse evolved on the *salvini-adspersus* group and has recently spread to *desmarestianus.* All species of *Liomys,* except *irroratus,* and *Heteromys desmarestianus* have six plantar tubercles; *L. irroratus* has only five plantar tubercles, which I believe is the derived condition, six being the primitive number.

A number of characters serve to distinguish members of the genus *Heteromys* from *Liomys*; probably the most important of these deal with the dentition. The lower premolars of *Liomys* are composed of but two lophids, whereas those of *Heteromys* are comprised of either three or four lophids. Accessory enamel islands are persistent in *Heteromys* but are found only in the youngest specimens of *Liomys*; also the median valley on the molars is persistent into adulthood in most species of *Heteromys,* whereas it is worn away in *Liomys* before adulthood is reached. Other characters that are unique to *Heteromys* are presence of the anopluran lice species *Fahrenholzia ferrisi, F. hertigi,* and *F. schwartzi,* naked soles on hind feet (except *H. gaumeri*), V-shaped interpterygoid fossa, and occupancy of areas of moist forests in Central America and México (except *H. gaumeri*).

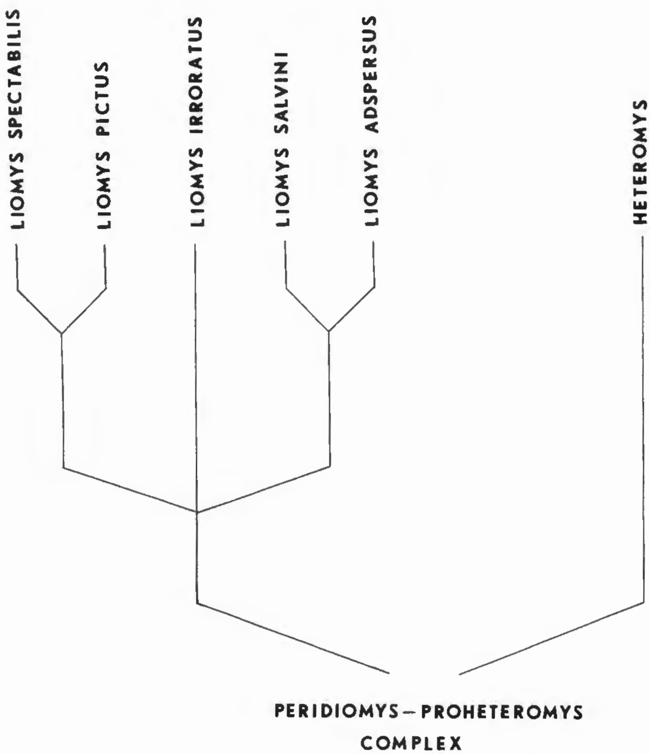


FIG. 65.—Hypothethical representation of the phylogenetic relationships among the five species of *Liomys* and their relationship to the genus *Heteromys*.

My concept of the phylogenetic relationships within the genus *Liomys* and their relationship to *Heteromys* based upon the preceding analyses is presented in Fig. 65. From early heteromyine stock of which the *Proheteromys-Peridiomys* complex is the most likely (see Wood, 1931, 1935), the genera *Liomys* and *Heteromys* had separate origins. The ancestor of the *Liomys* lineage probably most closely resembled the Recent species *Liomys irroratus*, but almost certainly differed from it in a number of ways. This basic stock underwent differentiation into three lines giving rise to the precursors of *irroratus*, the *salvini-adspersus* group, and the *pictus-spectabilis* group. If the degree of differentiation between the groups can be used as a gauge, it would appear that the three originated at approximately the same time. Within the *salvini-adspersus* and the *pictus-spectabilis* groups, there was a much more recent splitting to give rise to the Recent species. It seems most likely that these last differentiations occurred in relatively late Wisconsin time, but it is impossible to actually date any of these events because of the almost complete lack of a fossil record. The distribution patterns of the two groups that have recently undergone speciation suggest that these may have come about by what Brown (1957) termed centrifugal speciation. If this is true, *adspersus* and *spectabilis* would be expected to more nearly resemble the precursors of their respective groups, the species *salvini* and *pictus*, with their larger gene pool and consequently more opportunities for mutations and recombination, having essentially "evolved away from" this precursor. I have little evidence to present on either side of this question, but *adspersus* and *spectabilis* both are large-sized species as were many Pleistocene taxa and their chromosome compliment is slightly less differentiated from the ancestral condition (if parsimony is envoked) than is that of *pictus* and *salvini*. On the other hand, in most of the analyses above, when all characters were considered, *pictus* and *salvini*, within their respective groups, revealed more similarities to *irroratus* than did either *spectabilis* or *adspersus*. Although Jackson and Crovello (1971) have pointed out pitfalls in using some of the numerical analyses employed herein to deduce evolutionary relationships, these are presented along with my concept of phyletic relationships within the genus *Liomys* as the best estimate possible at this time based upon the available data. However, if fossil material becomes available in the future and additional biosystematic data are obtained, these results should be compared with the present model and, if necessary, the model modified in accord with new findings.

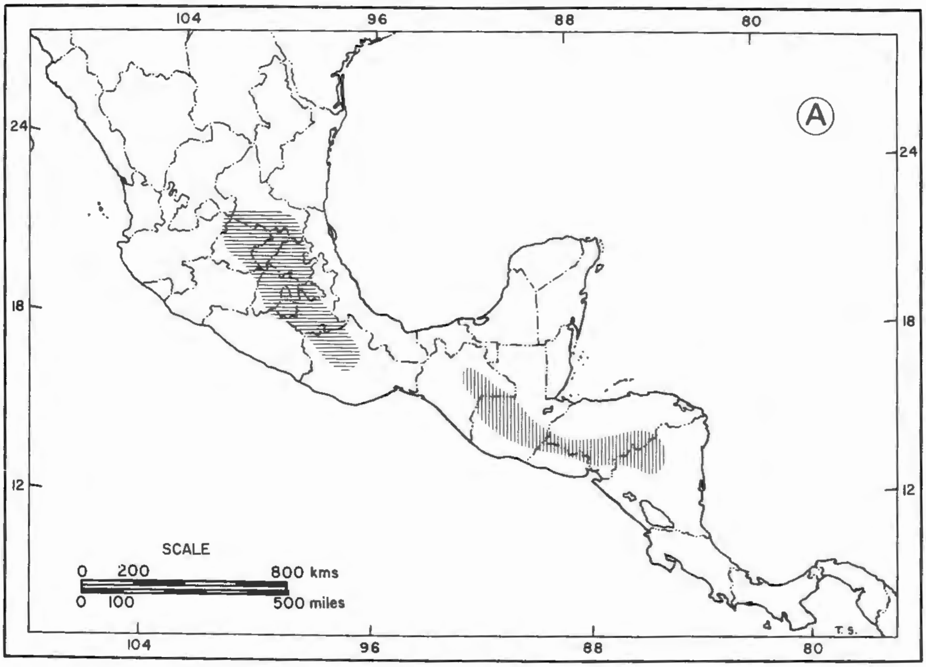
Zoogeographically, Recent members of the genus *Liomys* occur mainly in the Neotropical Region and the transition zone between the Neotropical and Nearctic regions, but portions of the ranges of *L. pictus* and *L. irroratus* are included in the Nearctic Region (Hershkovitz, 1958, 1969; Hooper, 1949). Members of the genus *Heteromys* occur exclusively in the Neotropical Region. In the classification of major units of North American rodent fauna proposed by Hooper (1949), *Liomys* would be included in both the Sonoran and tropical faunas, whereas *Heteromys* would be placed only in the tropical fauna. Biotic provinces are much less useful in describing the geographic range of these two genera because individual species range through several provinces (for example *Liomys irroratus* is found in Chihuahua-Zacatecas, Sierra Madre Occidental, Tamaulipas, Sierra Madre Oriental, Veracruz, Transverse Volcanic, and Sierra Madre del Sur—see Goldman and Moore, 1946) and the provinces of Central America (Ryan, 1963) are poorly defined because the ranges of many species are at best ill defined.

Essentially the picture that emerges is that members of the genus *Liomys* occur within, and just to the north of, the Neotropical Region and *Heteromys* is exclusively Neotropical in distribution (also see Baker, 1963). The next question that arises is what was the past zoogeographic history of these genera. Unfortunately, only an outline of this history is possible at present because the fossil record of these groups is poor and our knowledge of vegetational and geological history of México and Central America is only now emerging. It is evident that the evolutionary history of the family Heteromyidae has been tied to the developing aridity in the Great Plains and Southwest during the Miocene and Pliocene (Wood, 1935:230-236). Members of the subfamily Heteromyinae are known from as far north as Oregon and Nebraska, and from Florida during this time. However, the evolution of *Liomys* and *Heteromys* probably occurred to the south in México and Central America.

The ancestors of *Liomys* probably evolved on the southern Mexican Plateau in much the same areas as the southern part of the range of Recent *Liomys irroratus* (Fig. 66). Whether these animals evolved as the Madro-Tertiary Geoflora developed in this area (Axelrod, 1958, 1960) or simply evolved in the already developed flora cannot be stated at this time, but the distribution of *Liomys* is closely correlated with this flora. On the other hand, I believe *Heteromys* evolved in isolation from *Liomys* in Nuclear Central America (Lloyd, 1963; Stuart, 1966); members of this genus were evidently undergoing their evolution in areas of the Neotropical-Tertiary Geoflora. The exact reasons for the shift of *Heteromys* into a more mesic habitat than other members of the family can only be a matter of conjecture, but one reason may be that this was essentially the only habitat available in Nuclear Central America at the time. With the closing of the Panamanian Portal in the late Pliocene, *Heteromys* was able to enter northern South America (Hershkovitz, 1969:23).

Sometime probably in the early Pleistocene the ancestor of the *salvini-adspersus* group extended along the Pacific coast of Central America where the Madro-Tertiary Geoflora had developed as the result of increasing aridity caused by the uplift of Nuclear Central America beginning in the Pliocene (Fig. 66). Isolation of this group from other *Liomys* most likely was accomplished across the Isthmus of Tehuantepec, if conditions as suggested by Duellman (1960) occurred in the region during the Pleistocene. He believed that the Isthmus was never completely submerged during the Pleistocene, but that isolation was accomplished by a combination of fluctuations in sea level and climatic conditions. During glacial periods the lowlands of the Isthmus were probably more extensive and had more semiarid environments than at present because of the depressed sea level; these times would allow passage of lowland animals, but would result in isolation of highland taxa. Interglacial periods, on the other hand, would have been characterized by warmer temperatures, higher sea level, and moister conditions across the portion of the Isthmus that remained emergent; in these times lowland kinds would have been isolated with highland faunas being able to cross the Isthmus. This set of conditions easily explains the passage of *Liomys* across the Isthmus to the south, their subsequent isolation and speciation (Fig. 66), and the fact that members of the genus *Heteromys* were able to pass through the Isthmus to the north. During a glacial period, probably the Wisconsin, members of the *salvini-adspersus* group, because of the depressed sea level resulting in more extensive lowlands and arid conditions, were able to extend their

FIG. 66.—Some possible events resulting in speciation in the genus *Liomys*. A—Hypothetical distribution of precursors of *Liomys* in México and *Heteromys* in Chiapas and Central America. B—Increased geographic range of precursor of *Liomys* across Isthmus of Tehuantepec in response to increasing aridity. C—Isolation of precursors of *Liomys pictus*-group in western México, *Liomys salvini*-group in Central America, and *Liomys irroratus* on the Mexican Plateau probably in response to increasing moist conditions and rising sea level in vicinity of Isthmus of Tehuantepec. D—Distribution of Recent species of *Liomys*. See text for additional discussion. →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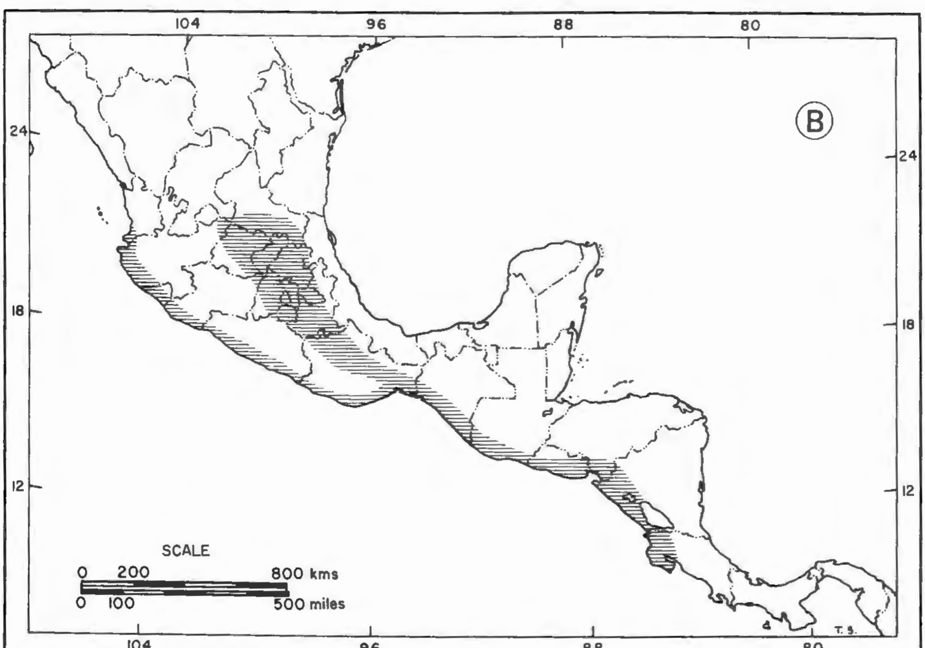
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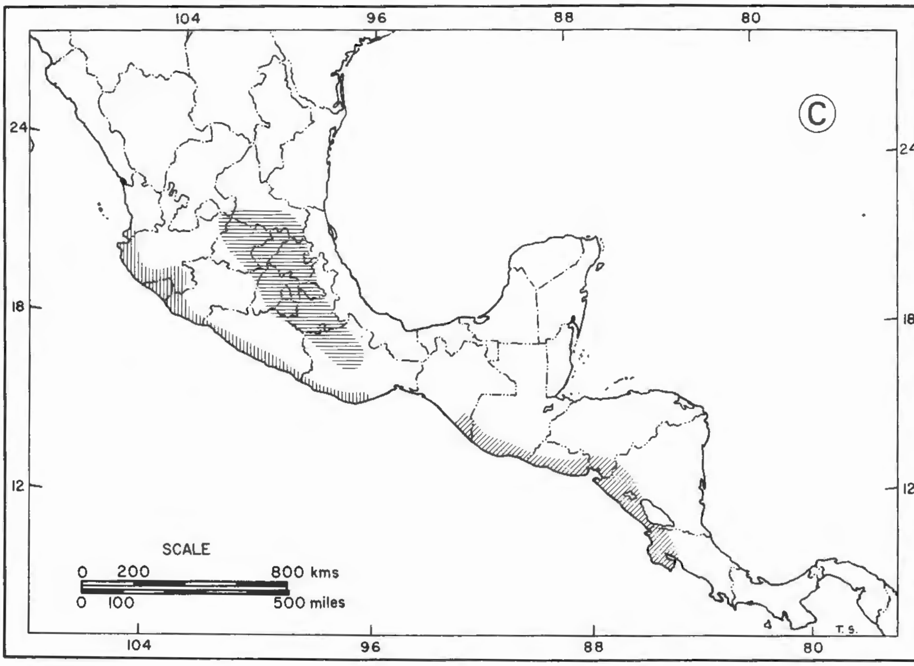

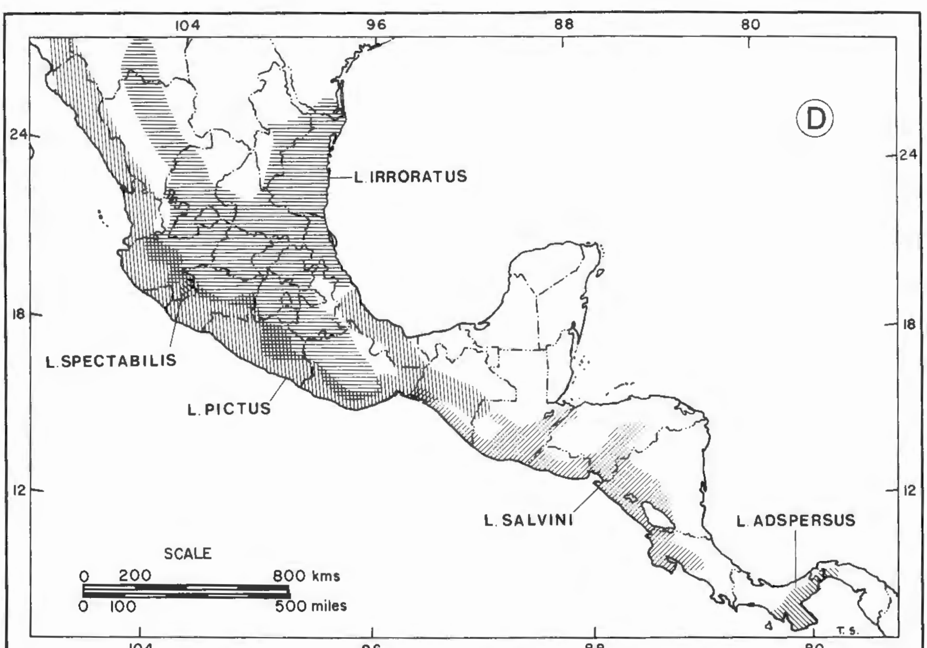

FIG. 66.—Continued.

range into the savannas of the Pacific coast of Panamá. The return of warmer and moister conditions and the restriction of the lowland by rising sea levels in the subsequent interglacial has resulted in isolation and speciation giving rise to *Liomys salvini* in most of Central America and *Liomys adspersus* in the savannas of Panamá. These species are separated today by tropical rainforest and quasi-rainforest in the vicinity of the Golfo Dulce region of Costa Rica and western Panamá (Wagner, 1964; Stuart, 1966). This distributional pattern is exhibited by other vertebrate groups, especially the herpetofauna (Duellman, 1966; Savage, 1966).

About the same time the precursor of the *salvini-adspersus* group entered Central America, the ancestors of the *pictus-spectabilis* group entered the Pacific Coast of México (Fig. 66) in that region termed the North Subtropical Sector by Baker (1967). What served to isolate this group is not clear, but most likely it was the mountain masses, Sierra Madre Occidental and Sierra Madre del Sur, of western México. Evidently *spectabilis* was isolated in interior drainage basins of Jalisco from the much more widespread *pictus* and subsequent to speciation *pictus* has reinvaded that area to become sympatric with *spectabilis*. The exact circumstances of this isolation and reinvasion are not clear at present, but probably they were associated with climatic fluctuations in the late Wisconsin and post-Wisconsin times. Another possible explanation that should not be disregarded is that *spectabilis* was isolated from *pictus* by volcanic activity associated with the Transverse Volcanic Belt. The geographic range of *spectabilis* lies just to the northeast of the Sierra Nevado de Colima and Volcán de Colima, and its isolation from *pictus* on the coast could have resulted from activity of these volcanos.

At the time other species were undergoing differentiation in western México and Central America, *Liomys irroratus* was evolving from the ancestral stock of the genus, more or less *in situ*, on the Mexican Plateau (Fig. 66).

During my study of this group, two factors have seemed to me to be most important in determining the distribution of Recent species of *Liomys* (Fig. 66). First, moisture appears to be a significant factor; as stated above several times, in areas of high moisture *Liomys* is replaced by members of the genus *Heteromys*. On the other hand, members of the genus are limited also by extreme aridity, because no species occur in areas receiving less than 250 millimeters of rain annually and most do not occur in areas receiving less than 500 millimeters of rain annually (data from Vivó Escoto, 1964).

Second, the presence of a congeneric species appears to form a significant barrier to dispersal. This would account for the restricted areas of sympatry between species and certain unusual patterns of distribution (such as only *L. pictus* occurring in the central valley of Chiapas where it appears to be a barrier to the entry of *L. salvini*). Essentially, the first species present would serve to block the entry of the second. A similar situation was noted by Russell (1968:758-760) among members of the closely related family Geomyidae.

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APPENDIX I—GAZETTEER

Names of geographic and topographic features listed below are those used in the text of this report. The primary sources for spellings and coordinates of localities were the gazetteers of the United States Board on Geographic Names (prepared by the Office of Geography, Department of Interior) for British Honduras (no. 16 issued March 1956), Costa Rica (no. 18 issued March 1956), Guatemala (no. 94 issued September 1965), El Salvador (no. 26 issued October 1956), Honduras (no. 27 issued October 1956), México (no. 15 issued February 1956), Nicaragua (no. 25 issued October 1956), and Panamá and the Canal Zone (no. 110 issued June 1969). If place-names were not found in the above-listed gazetteers, other sources used to locate them included: 1) The American Geographic Society's "Map of Hispanic America. . . . " scale 1:1,000,000, and its accompanying Index (1944); 2) Estados Unidos Mexicanos, Comisión Intersecretarial Coordinadora del Levantamiento de la Carta Geográfica de la República Mexicana, 1:500,000 (1957-1958); 3) a collection of maps entitled "Caminos de México," published by Compañia Hulera Euzkadi, S. A., third edition (1967); 4) México, Mapa Turistico de Carreteras elaborado por la Secretaría de Obras Publicas con la colaboración de Secretaría de Comunicaciónes y Transportes, Departamento de Turismo, y Petróleos Mexicanos (1966); 5) set of maps covering most of the country of Nicaragua, 1:50,000, available from Dirección General de Cartografía, Ministerío de Fomento, Managua, Nicaragua; 6) Mapa de la República de Guatemala, compilado por Federico P. de Torroella, litografía Arimany, Guatemala (1948); 7) Mapa de carreteras de Venezuela produced by the Creole Petroleum Corporation in 1966; 8) and various road maps prepared by petroleum companies, most notable of which are those for the Central American countries prepared by Esso Standard Oil, S. A. Any entry listed from one of these secondary sources is marked with an asterisk (*).

Places that could not be located directly, but that were located indirectly with reference to some other known feature, can be recognized because the word "approximately" is used in their designation. Names in brackets refer to other names or spellings of a given place that are frequently encountered in the literature or on maps. All latitudes are north of the equator and longitudes west of Greenwich. Sequence of countries, of states within México, and individual localities within the countries and states is alphabetical. Each locality listed for Texas is followed by the name of the county in which it is located, and localities in Central American countries are followed by the name of the departamento in which they are found.

Other general gazetteers dealing with the region covered herein are those of Choate (1970:312-317), Davis (1944:371-374), Hooper (1947:40-42, 1952: 220-249), and Musser (1964:1-5). Several of these contain brief ecological descriptions of localities. Other useful gazetteers that deal with individual states or countries are cited under the appropriate subheading below.

British Honduras

Roaring River, Cayo – 17°16′, 88°48′*
Spanish Lookout, Cayo – 17°13′, 88°59′

Costa Rica

Altos Escazú, San José – approximately 9°56′, 84°09′ (heights above the town of Escazú)
Bagaces, Guanacaste – 10°31′, 85°15′
Bebedero, Guanacaste – 10°22′, 85°12′
Boca del Barranca, Puntarenas – 9°58′, 84°44′*
Congrejal, San José – approximately 9°46′, 84°12′ (this locality is 5 mi. SSW San Ignacio, according to A. B. McPherson)
Esparta, Puntarenas – 9°59′, 84°40′
Filadelfia, Guanacaste – 10°26′, 85°34′
Finca Jiménez, Guanacaste – approximately 10°20′, 85°12′ (according to E. T. Hooper, Finca Jiménez is a part of the larger Finca Taboga and straddles the Río Higueron, 6 mi. S, 6 mi. W Las Cañas)
Las Cañas, Guanacaste – 10°25′, 85°07′
Liberia, Guanacaste – 10°38′, 85°27′
Los Higuerones, San José – approximately 9°56′, 84°09′ (small farms about Escazú)
Monte Verde, Puntarenas – approximately 10°19′, 84°49′ (a Quaker settlement near the junction of the provinces of Alajuela, Guanacaste, and Puntarenas, according to A. B. McPherson)
Pandora, Limón – 9°45′, 82°57′
Playa del Cocos, Guanacaste – 10°33′, 85°43′
Puerto Viejo, Heredia – 10°26′, 83°59′
Río Teopisco, 30 mi. S Nicaraguan border, Guanacaste – approximately 10°47′, 85°33′
Sabanilla de Pirrís, San José – 9°44′, 84°16′
San Francisco Esparta, Puntarenas – a town adjoining Esparta (see that locality for coordinates)
San Ignacio, San José – 9°48′, 84°09′
San José, San José – 9°56′, 84°05′
San Juanillo, Guanacaste – 10°02′, 85°44′
Santa Ana, San José – 9°56′, 84°11′
Santa Cruz, Guanacaste – 10°16′, 85°36′
Santa Rosa, Guanacaste – 10°51′, 85°38′
Tempate, Guanacaste – 10°24′, 85°44′
Tilarán, Guanacaste – 10°28′, 84°59′
Turrialba, Cartago – 9°54′, 83°41′
Villa Colón, San José – 9°55′, 84°14′

For additional information on localities in Cost Rica see Harris (1943:1-6) and Goodwin (1946:454-458).

El Salvador

Amate de Campo [Laguna Limpia], La Paz – approximately 13°24′, 89°07′
Barra de Santiago, Ahuachapán – 13°47′, 90°03′
Divisadero, Morazán – 13°36′, 88°04′
El Tablón, Santa Ana – approximately 14°15′, 89°35′ (this locality is on SE shore Lake Guija)
Finca Raquelina, Ahuachapán – approximately 13°52′, 89°48′
Hacienda Chilata, Sonsonate – 13°40′, 89°32′
Hacienda Nancuchiname, Usulután – approximately 13°25′, 88°41′
Hacienda San Antonio, Sonsonate – approximately 13°42′, 89°45′
Isla de la Cabra, Santa Ana – 13°51′, 89°34′* (in Lake Coatepeque)
Laguna de Guija, Santa Ana – 14°13′, 89°34′
Lake Coatepeque, Santa Ana – 13°52′, 89°33′
Lake Olomega, San Miguel – 13°19′, 88°04′
Los Planes [Planes de Renderos], San Salvador – 13°39′, 89°11′
Monte Cristo Mine, Morazán – approximately 13°36′, 88°05′ (this mine is 1½ mi. W Divisadero)
Mount Cacaquatique, San Miguel and Morazán – 13°46′, 88°13′
Pine Peak, La Union – approximately 13°17′, 87°55′ (this peak is 3 mi. W Volcán Cochagua)
Puerto del Triunfo, Usulután – 13°17′, 88°33′
Río Goascorán, La Union – approximately 13°31′, 87°44′
Río San Miguel, San Miguel – approximately 13°25′, 87°44′
San Salvador, San Salvador – 13°42′, 89°12′
Santa Tecla [Nueva San Salvador], La Libertad – 13°41′, 89°17′
Volcán San Miguel, San Miguel – 13°26′, 88°16′

For additional information on localities in El Salvador see Burt and Stirton (1961: 8-17).

Guatemala

Antigua, Sacatepéquez – 14°34′, 90°44′
Astillero, Santa Rosa – 13°51′, 90°21′
Cabañas, Zacapa – 14°56′, 89°48′
Cerro las Flores, Finca El Carnero, Jutiapa – 14°17′, 89°59′*
Chiquimulilla, Santa Rosa – 14°05′, 90°23′
Concepción del Mar, Escuintla – approximately 14°00′, 91°30′ (information about this locality was supplied by Joseph C. Moore)
Cuilapa, Santa Rosa – 14°17′, 90°18′
Dueñas, Sacatepéquez – 14°31′, 90°48′
El Rancho, El Progreso – 14°55′, 90°00′
Escuintla, Escuintla – 14°18′, 90°47′
Finca El Progreso, Santa Rosa – 14°13′, 90°26′
Finca Los Arcos, Escuintla – 14°14′, 90° 51′*
Finca Valle-Lirios, Escuintla – approximately 13°56′, 91°00′ (information about this locality was supplied by C. O. Handley, Jr.)
Granados, Baja Verapaz – 14°55′, 90°31′
Gualán, Zacapa – 15°08′, 89°22′
Guatemala, Guatemala – 14°38′, 90°31′
Hacienda California, San Marcos – 14°33′, 92°10′
Iztapa, Escuintla – 13°56′, 90°43′
Jocotán Chiquimula – 14°49′, 89°23′
Km. 24 on highway S Guatemala City, Guatemala – approximately 14°28′, 90° 38′
Km. 27 on highway S Guatemala City, Guatemala – approximately 14°27′, 90° 39′
Km. 33 on highway S Guatemala City, Escuintla – approximately 14°25′, 90° 40′
Km. 52 on highway S Guatemala City, Escuintla – approximately 14°19′, 90° 46′
Lake Amatitlán, Guatemala – 14°27′, 90° 34′
Lake Atescatempa, Jutiapa – 14°12′, 89°42′
La Primavera, Alta Verapaz – approximately 15°25′, 90°29′ (see Stuart, 1950: map 2, for location of this finca)
Masagua, Escuintla – 14°12′, 90°51′
Mazatenango, Suchitepéquez – 14°32′, 91° 30′
Monogoy [Mongoy], Jutiapa – 14°15′, 89° 43′
Nentón, Huehuetenango – 15°48′, 91°45′
Progreso, El Progreso – 14°51′, 90°04′
Puebla, Izabal – 15°18′, 89°00′*
Puente Punta Gordo, El Progreso – approximately 14°48′, 90°12′ (this bridge is located at km. 51 on the highway from Guatemala City to Puerto Barrios, according to Jones, 1966:469)
Rabinal, Baja Verapaz – 15°06′, 90°27′
Río Grande, 152 km. NE Guatemala City, Zacapa – approximately 15°06′, 89°24′ (this locality is approximately 17 mi. NE Río Hondo)
Sacapulas, El Quiché – 15°20′, 91°04′
Salamá, Baja Verapaz – 15°06′, 90°16′
San Cristóbal [Frontera], Jutiapa – 14°11′, 89°40′
San José, Escuintla – 13°55′, 90°49′
San Lucas, Sololá – 14°38′, 91°08′
Santiago Sacatepéquez, Sacatepéquez – 14° 38′, 90°41′
Tiquisate, Escuintla – 14°17′, 91°22′
Trujillo, Zacapa – 14°57′, 89°49′
Volcán San Lucas, Sololá – 14°37′, 91°07′*
Yepocapa, Chimaltenango – 14°30′, 90°57′

For additional information on localities in Guatemala see Griscom (1932:413-425), Stuart (1954:36-41), and Jones (1966:467-469).

Honduras

Catacamas, Olanche – 14°54′, 85°56′
Cerro de los Cuches, Francisco Morazán – approximately 13°48′, 87°14′ (this locality is 4 km. SE Sabana Grande)
Comayagüela, Francisco Morazán – 14° 05′, 87°13′
El Caliche Orica, Francisco Morazán – approximately 14°31′, 87°03′ (this locality is W Orica)
El Zapote, Francisco Morazán – approximately 13°45′, 87°15′ (this locality is 7 km. S Sabana Grande)
Escuela Agricultura Panamericana, Francisco Morazán – 13°59′, 86°59′ (this school is on the Tegucigalpa-Danli road on the Yeguare River)*
Hatillo, Francisco Morazán – 14°88′, 87°10′
La Cueva Archaga, Francisco Morazán – approximately 14°17′, 87°13′ (this locality is near Cerro Archaga)
La Flor Archaga, Francisco Morazán – approximately 14°15′, 87°15′ (this is a village on Talanga road E Cerro Archaga)

La Piedra de Jesús, Francisco Morazán – approximately 13°47′, 87°15′ (this place is 5 km. S Sabana Grande)
La Venta, Francisco Morazán – 14°18′, 87° 10′
Monte Redondo, Francisco Morazán – approximately 14°16′, 87°15′ (this locality is 15 mi. NNW Tegucigalpa, according to Hooper, 1952:227)
Sabana Grande, Francisco Morazán – 13° 50′, 87°15′
San Pedro Sula, Cortés – 15°27′, 88°02′
Tegucigalpa, Francisco Morazán – 14°06′, 87°13′
Toncontín, Francisco Morazán – 14°02′, 87°13′*

For additional information on localities in Honduras see Goodwin (1942:108-111).

MEXICO

Aguascalientes

Aguascalientes – 21°53′, 102°18′
Calvillo – 21°51′, 102°43′
Chicalote – 22°02′, 102°16′
La Labor – approximately 21°58′, 102°42′ (according to the specimen label, this locality is 9 mi. by road N Calvillo)

Campeche

Champotón – 19°21′, 90°43′
Escárcega – 18°37′, 90°43′

Chiapas

Altamirano – 16°53′, 92°09′
Arriaga – 16°14′, 93°54′
Berriozábal – 16°48′, 93°16′
Bochil – 16°59′, 92°55′
Cacahuatál – approximately 16°29′, 93°59′ (this locality is 3 km. eastward from Rizo de Oro or Los Amates, 16°28′, 94°00′*, on the road to Tuxtla Gutiérrez, according to information supplied by A. L. Gardner)
Cerro Tres Picos – 16°12′, 93°37′*
Chiapa de Corzo [Chiapa] – 16°42′, 93°00′
Cinco Cerros – approximately 16°31′, 93° 57′ (this place is approximately 6 to 8 km. from Rizo de Oro toward Tuxtla Gutiérrez, according to information supplied by A. L. Gardner)
Cintalapa – 16°44′, 93°43′
Ciudad Cuauhtémoc – 15°37′, 92°00′
Comitán – 16°15′, 92°08′
Escuintla – 15°20′, 92°38′
Finca El Paraío – 17°07′, 91°54′*
Guatimoc [Cuatimoc] – 15°02′, 92°09′
Huehuetán – 15°01′, 92°22′
Huixtla – 15°08′, 92°28′
Jaltenango – 15°55′, 92°43′
La Trinitaria – 16°07′, 92°03′
Madre Mía – 16°08′, 93°39′
Maspastepec – 15°26′, 92°54′
Ocozocoautla – 16°46′, 93°22′
Ortiz Rubio – 16°22′, 93°52′*
Palenque – 17°31′, 91°58′
Pan-American Highway, 16 mi. N Guatemalan border – approximately 15°50′, 91°58′
Pijijiapan – 15°42′, 93°14′
Pueblo Nuevo [Pueblo Nuevo Solistahuacán] – 17°06′, 92°53′
Puerto Arista – 15°56′, 93°48′
Puerto Madero – 14°44′, 95°25′
Sabena de San Quintín – 16°24′, 91°20′
San Bartolomé [Venustiano Carranza] – 16°21′, 92°33′
San Clemente – 16°26′, 93°43′
San Gregorio – 15°55′, 92°10′
San Miguel – approximately 16°14′, 93°34′
San Vincente – 16°00′, 91°46′
Talisman – 14°58′, 92°09′
Tapachula – 14°54′, 92°17′
Tonalá – 16°04′, 93°45′
Tuxtla Gutiérrez – 16°45′, 93°07′
Unión Juárez – 15°04′, 92°05′
Valley of Jiquipilas – approximately 16°40′, 93°35′ (according to Goldman, 1951:116, specimens labeled in this manner were taken along a tributary of the Río de la Venta at Rancho San Ricardo)
Villa Flores – 16°14′, 93°14′

Chihuahua

Batopilas – 27°01′, 107°44′
Jiménez – 27°08′, 104°55′
Parral [Hidalgo del Parral] – 26°56′, 105° 40′
Santa Rosalía [Ciudad Camargo] – 27°40′, 105°10′

Colima

Agua Zarca – 19°13′, 103°55′
Armería – 18°56′, 103°58′
Cerro Chino – 19°12′, 104°00′*
Colima – 19°14′, 103°43′
Comatlán [de Miraflores] – 19°13′, 104° 14′*

Hacienda Magdelena [Pueblo Juárez] – 19° 10′, 103°55′*
Hacienda San Antonio – 19°27′, 103°44′ (this locality is 26 mi. N Colima, according to Goldman, 1951:136)
La Gloria – approximately 19°10′, 104°12′ (this place is 29 km. W Pueblo Juárez, according to specimen label)
Las Juntas – approximately 19°10′, 104°10′ (this locality is 26 km. W Pueblo Juárez, according to specimen label)
Las Juntas – approximately 19°07′, 103°53′ (this locality is 5 km. SE Pueblo Juárez, according to specimen label)
Las Lomas – approximately 19°11′, 103°45′ (this place is 3 or 4 mi. S Colima on highway to Manzanillo, according to A. L. Gardner)
Manzanillo – 19°03′, 104°20′
Paso del Río – 18°57′, 103°56′
Pueblo Juárez – see Hacienda Magdelena
Quesería – 19°22′, 103°35′
Santiago – 19°07′, 104°21′
Tlapeixtes – approximately 19°04′, 104°18′ (this locality is 4 km. ENE Manzanillo, according to Gardner, 1966:4-5)
Trapichillos – 19°08′, 103°30′*

For additional information on localities in Colima see Schaldach (1963:7-12).

Distrito Federal

Cerro Xaltepec – 19°19′, 99°02′*
Ciudad Universitaria – 19°20′, 99°11′*
Contreras – 19°18′, 99°17′
México – 19°24′, 99°09′
Pedregal de San Angel – 19°19′, 99°11′ (this is the pedregal to the south of Ciudad Universitaria)*
San Gerónimo [San Jerónimo] – 19°20′, 99°14′*
San Gregorio Altapulco – 99°03′, 19°15′*
San Mateo Xalpa [San Mateo Jalpa] – 19° 14′, 99°07′*
Tlalpan [Tlalpam] – 19°17′, 99°10′
Xochitepec – 19°16′, 99°07′*
Zapotitlán – 19°18′, 99°02′

Durango

Canatlán – 24°31′, 104°37′
Chacala – 24°50′, 106°45′
Chorro – 24°16′, 104°27′
Durango – 24°02′, 104°40′
Indé – 25°54′, 105°13′
Navarro – 26°42′, 106°12′
Pueblo Nuevo – 23°23′, 105°23′
Río Sestín – approximately 26°07′, 105°40′ (this is the location of the town of Sestín, which is probably near the collecting site of J. H. Batty, see J. A. Allen, 1903:591)
Rodeo – 25°11′, 104°34′*
Rosario – 26°31′, 105°40′
Tepehuanes [Santa Catarina de Tepehuanes] – 25°21′, 105°44′

For additional information about localities in Durango see Baker and Greer (1962:54-55).

Guanajuato

Acámbaro – 20°02′, 100°43′ (railroad station)
Moroleón – 20°08′, 101°12′
Salvatierra – 20°13′, 100°53′
San José [San José Iturbide] – 21°00′, 100° 23′
Silao – 20°56′, 101°26′

Guerrero

Acahuizotla – 17°23′, 99°27′
Acapulco – 16°51′, 99°55′
Acapulco Bay – 16°50′, 99°53′
Agua del Obispo – 17°13′, 99°31′*
Almolonga – 17°36′, 99°16′
Apaxtla – 18°09′, 99°52′
Ayotzinapa [Ayusinapa on specimen label] – 17°33′, 98°45′
Cacahuamilpa – 18°41′, 99°30′
Chapa – 18°19′, 99°49′
Chilpancingo – 17°33′, 99°30′
Cocula – 18°14′, 99°40′
Colotlipa – 17°25′, 99°09′
El Limón – 18°05′, 101°40′
El Rincón – 17°19′, 99°28′
Iguala – 18°21′, 99°32′
Infiernillo – 18°09′, 102°09′
Los Sabinos – 18°22′, 99°46′*
Mazatlán – 17°27′, 99°29′
Mexcala [Mezcala] – 17°56′, 99°37′
Ojo de Agua de Chapa – approximately 18°19′, 99°51′ (this locality is 5 km. SE Teloloapan, according to specimen labels)
Ometepec – 16°41′, 98°25′
Omilteme [Omiltemi] – 17°30′, 99°40′
Pie de la Cuesta – 16°54′, 99°58′
Río Balsas [Balsas] – 17°59′, 99°47′
Sacacoyuca – 18°14′, 99°33′

Sihuatanejo Bay [Bahía de Zihuatanejo] – 17°37′, 101°34′
Sochi [apparently an abbreviation for Xochihuehuetlán] – 17°55′, 98°26′
Taxco [de Alarcón] – 18°33′, 99°36′
Teloloapan – 18°21′, 99°51′
Texcalzintla – approximately 18°25′, 99°54′ (this locality is 6 km. NNW Teloloapan, according to specimen labels)
Tierra Colorada – 17°10′, 99°35′
Tixtla – 17°35′, 99°26′
Tlalixtaquilla – 17°21′, 98°28′
Tlapa – 17°33′, 98°33′
Tomatal – 18°19′, 99°30′
Xochipala – 17°49′, 99°37′
Yerbabuena – 18°27′, 99°54′*
Zacatula – 17°59′, 102°09′
Zihuatanejo – 17°38′, 101°33′
Zumpango [del Río] – 17°39′, 99°30′

For additional information on some localities in Guerrero see Davis and Dixon (1959: 79-80).

Hidalgo

Actopan – 20°16′, 98°56′
Epazoyucan – 20°02′, 98°38′
Ixmiquilpan – 20°29′, 99°14′
Maguey Verde – approximately 20°49′, 99°16′ (this place is 8½ mi. NE Zimapán, according to specimen label)
Marqués – 20°19′, 99°35′*
San Agustín – 20°04′, 99°05′
Tula [de Allende] – 20°03′, 99°21′
Zacaultipán – 20°39′, 98°36′
Zimapán – 20°45′, 99°21′

Jalisco

Acatlán [de Juárez] – 20°26′, 103°38′
Amatitán – 20°50′, 103°43′
Ameca – 20°33′, 104°02′
Arroyo de Gavalan – approximately 20°48′, 104°29′ (supposedly 20 mi. W San Marcos, according to J. A. Allen, 1906:237; however, this may not be correct)
Arroyo de Plantanar – not exactly located, but is near Amatlán de Cañas, Nayarit (see J. A. Allen, 1906:237)
Atemajac [del Valle] – 20°44′, 103°20′*
Atenqueque – 19°31′, 103°30′
Autlán [de Navarro] – 19°46′, 104°22′
Ayo el Chico – 20°32′, 102°21′
Barranca de Tule, Sierra Nayarit – not exactly located, but may be in vicinity of 21°57′, 103°56′
Barro de Navidad [Barra de Navidad and Navidad] – 19°12′, 104°41′
Belén de Refugio – 21°31′, 102°25′
Bolaños – 21°41′, 103°47′
Chamela Bay – 19°33′, 105°07′
Chapala – 20°18′, 103°12′
Cihuatlán – 19°14′, 104°35′
Ciudad Guzmán [Zapotlán] – 19°41′, 103°29′
Contla – 19°45′, 103°05′
Comanja de Corona – 21°19′, 101°42′
Cuitzamala [Cuitzmala] – 19°23′, 104°59′*
Durazno – not exactly located, but approximately 19°32′, 104°16′ (based on M. R. Lee's field notes)
El Zapote – 20°31′, 103°18′
Emiliano Zapata – approximately 19°21′, 104°58′
Encarnación [de Díaz] – 21°31′, 102°14′
Estancia – not exactly located, but is near Amatlán de Cañas, Nayarit (see J. A. Allen, 1906:237)
Etzatlán – 20°46′, 104°05′
Guadalupe de Victoria – 21°37′, 101°38′ (given as Matanzas on current maps, according to information supplied by R. G. Webb)
Guadalajara – 20°40′, 103°20′
Huascato – 20°32′, 102°14′
Huejúcar – 22°21′, 103°13′
Huejuquilla [el Alto] – 22°36′, 103°52′
Ixtapa – 20°42′, 105°15′
Jalostotitlán – 21°12′, 102°28′
Jazmín – 19°39′, 103°48′
Jilotlán de los Dolores – 19°12′, 103°13′
Jocotepec – 20°18′, 103°26′
La Cuesta – 20°10′, 104°51′
La Cumbre – approximately 19°42′, 104°22′ (this place is 9 mi. SSW Autlán de Navarro, according to Schaldach, 1963: 12)
Lagos de Moreno – 21°21′, 101°55′
La Laguna, Sierra de Juanacatlán – 20°39′, 104°47′
La Primavera – 20°40′, 103°32′*
La Resolana – 19°34′, 104°31′
Las Canoas – 19°37′, 103°32′ (this locality is 40 mi. W Tuxpan, according to J. A. Allen, 1906:238; however, I feel that this is more likely the small town with the same name that is located 10 km. NW Tuxpan)
La Venta – 20°44′, 103°33′
Limón – 19°52′, 104°07′

Magdelena – 20°55′, 103°57′
Mascota – 20°32′, 104°49′
Mazamitla – 19°55′, 103°02′
Melaque – 19°13′, 104°43′
Mezquitic – 22°23′, 103°41′
Milpillas –20°44′, 104°56′
Navidad – see Barro de Navidad
Navidad Bay – 19°12′, 104°43′
Nevado de Colima – 19°33′, 103°38′
Ocotlán – 20°21′, 102°46′
Piguamo – see Pihuamo
Pihuamo [Piguamo] – 19°15′, 103°23′
Platanar [Plantinar] – 19°28′, 103°27′
Puerto Vallarta – 20°37′, 105°15′
Purificación – 19°43′, 104°38′
Río Ameca – not exactly located, but is near Amatlán de Cañas, Nayarit (see J. A. Allen, 1906:237)
Río Santa María – not exactly located, but is near Amatlán de Cañas, Nayarit (see J. A. Allen, 1906:237)
Sal se Puedes – not exactly located, but is in mountains of west-central Jalisco, possibly near Talpa de Allende (see J. A. Allen, 1906:237)
San Gabriel [Venustiano Carranza] – 19° 44′, 103°47′
San Marcos – 20°47′, 104°11′ (*Liomys irroratus* locality)
San Marcos – 19°25′, 103°28′ (*Liomys pictus* locality)
San Sebastián – 20°47′, 104°51′
Santa Cruz de las Flores – 20°29′, 103°30′
Soyatlán del Oro – 20°20′, 104°15′ (information about this locality was supplied by A. L. Gardner)*
Tala – 20°40′, 103°42′
Tamazula – 19°38′, 103°15′
Tapalpa – 19°57′, 103°46′
Tecalitlán – 19°26′, 103°15′
Tecomate – 19°35′, 104°28′
Tenacatita – 19°17′, 104°47′
Tenacatita Bay – 19°17′, 104°50′
Tepatitlán [de Morelos] – 20°49′, 102°44′
Tequila – 20°54′, 103°47′
Teuchitlán – 20°41′, 103°52′
Tizapán [Tzipan on specimen labels] – 20° 10′, 103°04′
Tonalá – 20°37′, 103°14′
Tuxpan – 19°33′, 103°24′
Unión de San Antonio – 21°06′, 101°58′
Villa Guerrero – 21°59′, 103°36′
Wakenakili Mountains – not exactly located, but is in the mountains of west-central Jalisco, possibly near Talpa de Allende (see J. A. Allen, 1906:238)
Yahualica – 21°08′, 102°51′
Zapotiltic – 19°37′, 103°26′
Zapotlán – see Ciudad Guzmán
Zapotlanejo – 20°38′, 103°04′

México

Atlacomulco [de Fabela] – 19°48′, 99°53′
Ayotla – 19°19′, 98°55′
Barrientos – 19°35′, 99°11′*
Cerro la Caldera – approximately 19°20′, 98°57′
Chilpa – 19°38′, 99°10′*
Ecatepec [Morelos] – 19°35′, 99°04′
Hacienda Córdoba – approximately 19°20′, 98°43′ (this hacienda is 35 mi. ESE Mexico City on Mexico City-Puebla highway, according to Hooper, 1947:42)
San Rafael – 19°14′, 98°45′
Temascaltepec [de González] – 19°02′, 100°03′
Teotihuacán [San Juan Teotihuacán] – 19°41′, 98°52′
Tenancingo [de Degollado] – 18°58′, 99°35′
Texcoco [de Mora] – 19°31′, 98°53′
Tlalpitzahuac [Tlalpizahua on specimen label] – 19°20′, 98°56′
Tlalmanalco [de Veláquez] – 19°13′, 98° 48′
Tlalnepantla [de Galeana] – 19°33′, 99°12′
Valle de Bravo – 19°11′, 100°08′
Zoquiapan – 19°19′, 98°51′

Michoacán

Agua Blanca – not exactly located, but according to W. H. Osgood's field notes this locality is "near Jungapeo [19°27′, 100° 29′] and Zitácuaro [19°26′, 100°21′]" (information supplied by Joseph C. Moore)
Apatzingán – 19°05′, 102°15′
Arteaga – 18°28′, 102°25′
Carapan – 19°52′, 102°03′
Coalcomán – 18°47′, 103°09′
Cuitzeo [del Provenir] – 19°59′, 101°09′
Dos Aguas – approximately 18°45′, 102°55′ (this lumber camp is on the eastern slope of Cerro de Barolosa, located about 22 km. WNW Aguililla, according to Duellman, 1961:135)
El Atuto – approximately 18°10′, 102°09′ (this locality is 3 km. NE Infiernillo, Guerrero, according to specimen label)

Jacona – 19°57′, 102°16′
La Huacana – 18°58′, 101°49′
La Mira – 18°01′, 102°20′
La Palma – 20°09′, 102°46′
La Salada – approximately 18°51′, 101°55′ (this ranch is 40 mi. S Uruapan, according to Goldman, 1951:190)
Los Reyes – 19°35′, 102°29′
Melchor Ocampo – 17°59′, 102°11′
Morelia – 19°42′, 101°07′
Pátzcuaro – 19°31′, 101°36′
Queréndaro – 19°53′, 100°54′ (railroad station)
Quiroga – 19°40′, 101°32′
Tacámbaro – 19°14′, 101°28′
Tancítaro – 19°20′, 102°22′
Tarecuato – 19°51′, 102°29′
Tinqüindín [de Argándar] – 19°45′, 102°29′
Tumbiscatio – 18°31′, 102°21′
Tzitzio – 19°34′, 100°55′
Zamora [de Hidalgo] – 19°59′, 102°16′

For additional information on localities in Michoacán see Hall and Villa (1949:438) and Duellman (1961:129-141).

Morelos

Alpuyeca – 18°44′, 99°16′
Axochiapan – 18°30′, 98°46′
Cuautla – 18°48′, 98°57′
Cuernavaca – 18°55′, 99°15′
Huajintlán – 18°36′, 99°25′
Huitzilac – 19°02′, 99°16′
Jonacatepec – 18°41′, 98°48′
Michapa – 18°42′, 99°29′*
Puente de Ixtla – 18°37′, 99°20′
Tehuixtla – 18°33′, 99°16′
Temilpa – 18°41′, 99°06′
Temixco – 18°50′, 99°14′
Tepoztlán – 18°59′, 99°06′
Tequesquitengo – 18°36′, 99°16′
Tetecala – 18°43′, 99°24′
Yautepec – 18°53′, 99°04′

Nayarit

Acaponeta – 22°30′, 105°22′
Aticama – 21°29′, 105°13′
Amatlán de Cañas – 20°52′, 104°27′
Compostela – 21°14′, 104°55′
Huajicori – 22°39′, 105°18′
Ixtlán del Río – 21°02′, 104°22′
Jalisco – 21°27′, 104°54′
Jalisco-Nayarit border on Mexican Highway 15 – 21°03′, 104°13′*
La Cuchara – approximately 22°30′, 104°49′ (according to specimen label, this locality is "approximately 40 mi. E Acaponeta")
Las Varas – 21°10′, 105°10′
Navarrete – 21°39′, 105°07′
Ojo de Agua – not exactly located, but is near Amatlán de Cañas (see J. A. Allen, 1906:237)
Pedro Pablo – approximately 22°29′, 105°05′ (according to Goldman, 1951:202, this village is 22 mi. E Acaponeta along the western slope of the Sierra de Teponahuasta)
Platanares – 21°57′, 105°01′
Playa Novilleros – approximately 22°22′, 105°39′
Rancho Palo Amarillo – not exactly located, but is near Amatlán de Cañas (see J. A. Allen, 1906:237)
Rosamorada [Rosa Morada] – 22°08′, 105°12′
Ruiz – 21°57′, 105°09′
San Blas – 21°31′, 105°16′
San Francisco – 20°57′, 105°21′
San José del Conde – 21°05′, 104°44′
San Miguel – 20°20′, 105°17′
Santa Isabel – 21°10′, 104°37′
Santiago – 21°49′, 105°13′
Tepic – 21°30′, 104°54′
Tuxpan – 21°57′, 105°18′
Valle de Banderas – 20°49′, 105°17′

Nuevo León

Allende – 25°17′, 100°01′
Aramberri – 24°06′, 99°49′
Ascensión – 24°20′, 99°55′
Cerro de la Silla – approximately 25°39′, 100°14′ (this mountain is 6 mi. E Monterrey, according to Goldman, 1951:206)
China – 25°42′, 99°14′
General Teran – 25°16′, 99°41′
Ibarilla – 24°28′, 99°41′*
Iturbide – 24°44′, 99°44′
Linares – 24°52′, 99°34′
Montemorelos – 25°12′, 99°49′
Monterrey – 25°40′, 100°19′
Ojo de Agua – 24°55′, 100°11′*
Pablillo – 24°36′, 99°59′
San Francisco [Javier] – 24°59′, 100°21′
San Josecito Cave – near Aramberri
San Pedro Santiago – 25°22′, 100°07′
Zaragoza – 23°58′, 99°46′

Oaxaca

Agua Blanca – 16°41′, 95°45′
Aguaje Guayabo [Portillo Guayabo] – approximately 16°61′, 95°33′
Aguaje las Animas – approximately 16°15′, 95°22′
Aguaje Sapotal – approximately 16°21′, 95° 32′
Aguaje Tres Cabezas – approximately 16° 21′, 95°27′
Angeles Bay – 15°40′, 96°28′*
Buena Vista [San Dionisio del Mar] – 16° 20′, 94°45′
Candeleria – 15°54′, 96°30′*
Cerro Calderona – 16°23′, 95°21′*
Cerro de Tigre – approximately 16°21′, 95° 14′
Cerro Ocotepec – approximately 16°25′, 95° 43′
Cerro Palma de Oro – approximately 16°18′, 95°32′
Cerro San Felipe – 17°10′, 96°41′*
Cerro San Pedro – approximately 16°18′, 95°28′
Cerro Sombrerito – approximately 16°16′, 95°27′
Cerro Verde – approximately 16°35′, 95°36′
Chacalapa – 15°49′, 96°28′
Chahuites – 16°17′, 94°11′
Chicapa – 16°26′, 94°49′
Chivaguela – 16°28′, 96°12′
Chontecomatlán – 16°15′, 96°01′
Cuicatlán – 17°48′, 96°58′
Cycad Camp [km. 233 Oaxaca-Puerto Escondido Road] – approximately 15°59′, 97°06′
Ejutla [de Crespo] – 16°34′, 99°44′
El Bambita – approximately 16°20′, 95°35′
El Campanario – 16°45′, 95°07′*
Escondido Bay – 15°51′, 97°05′*
Escurano – approximately 16°25′, 95°27′
Gueladú – approximately 16°29′, 95°18′
Guichicovi – 16°58′, 95°06′
Guichina – approximately 16°27′, 96°06′
Guiengola – 16°21′, 95°20′*
Huajuapan de León [Huajuapam] – 17° 48′, 97°46′
Huilotepec – 16°14′, 95°09′
Isthmus of Tehuantepec, 8 mi. S Veracruz-Oaxaca state line – approximately 17°15′, 95°03′
Ixcuintepec – 16°56′, 95°42′
Jalapa – 16°30′, 95°28′
Jamaica Junction [km. 212 Oaxaca-Puerto Escondido Road] – approximately 16°09′, 97°06′
Jamiltepec – 16°17′, 97°49′
Jicotlán – 17°48′, 97°28′
Juchatengo – 16°21′, 97°06′
Juchitán – 16°27′, 95°01′
Km. 136 Oaxaca-Puerto Escondido Road [Turpentine Camp] – approximately 16° 24′, 97°05′
Km. 177.2 Oaxaca-Puerto Escondido Road – approximately 16°17′, 97°07′
Km. 183 Oaxaca-Puerto Escondido Road – approximately 16°16′, 97°07′
Km. 198 Oaxaca-Puerto Escondido Road – approximately 16°12′, 97°06′
Km. 212½ Oaxaca-Puerto Escondido Road – approximately 16°09′, 97°06′
Km. 214 Oaxaca-Puerto Escondido Road [Río Ranas] – approximately 16°07′, 97°06′
Km. 123 Putla-Tlaxiaco Road – approximately 17°05′, 97°51′
Km. 135 Putla-Tlaxiaco Road – approximately 17°03′, 97°53′
La Chacahua – approximately 16°23′, 95° 59′
Lachao – see San Juan Lachao
La Cima [km. 184 Oaxaca-Puerto Escondido Road] – approximately 16°16′, 97° 07′
La Concepción – approximately 17°02′, 97° 52′
Lagunas – 16°48′, 95°04′
La Mata – 16°38′, 95°00′
La Parada – approximately 17°08′, 95°30′ (this localtiy is 15 mi. NE Oaxaca, according to Goldman, 1911:54)
Las Cuevas – approximately 16°26′, 95°21′
Las Lagunas de Sol y Luna – approximately 16°28′, 94°12′
Las Minas – approximately 16°21′, 94°07′
Las Tejas – approximately 16°20′, 95°22′
La Ventosa – 16°33′, 94°57′
Limón – approximately 16°20′, 95°29′
Llano Grande – 16°28′, 98°18′*
Matatlán [Santiago Matatlán] – 16°52′, 96°53′
Mesones – 16°55′, 97°58′
Miahuatlán [de Porfirio Diaz] – 16°20′, 96°36′
Mitla – 16°55′, 96°24′
Mixtequilla – 16°22′, 95°15′
Monte Alban – 17°02′, 96°45′*

Mount Zempoaltepec [Zempoaltépetl or Cempoaltépetl] – 17°10′, 95°59′
Nejapa – 16°37′, 95°59′
Nizanda – 16°40′, 95°02′
Nopala [Santos Reyes Nopala] – 16°06′, 97°10′
Oaxaca [de Juárez] – 17°03′, 96°43′
Ocotita – approximately 16°26′, 95°23′
Pinotepa – see Pinotepa Nacional
Pinotepa de Don Luis – 16°25′, 97°55′
Pinotepa Nacional [Pinotepa] – 16°19′, 98°01′
Pluma [Pluma Hidalgo] – 15°55′, 96°24′
Portillo Guayabo – see Aguaje Guayabo
Portillo Zapote – approximately 16°18′, 95°36′
Pozo Río – approximately 16°20′, 95°18′
Puerto Angel – 15°40′, 96°29′
Puerto Escondido – 15°51′, 97°06′*
Putla – 17°02′, 97°56′
Reforma – 16°24′, 94°28′
Río Chile – approximately 16°25′, 95°37′
Río Grande – not exactly located, but may be near 16°21′, 95°59′
Río Guajolote – not exactly located, but near the Río Jalatengo and Río Molino (see Schaldach, 1966:286-287)
Río Jalatengo [km. 178 on Oaxaca-Puerto Angel Road] – approximately 15°58′, 96°27′
Río Molino – approximately 16°02′, 96°29′ (see Schaldach, 1966:286-287)
Salazar – 16°25′, 95°20′
Salina Cruz – 16°10′, 95°12′
San Andrés Chicahuaxtla – 17°10′, 97°50′
San Antonio – 16°15′, 95°28′
San Bartolo – see San Bartolo Yautepec
San Bartolo Yautepec – 16°26′, 95°59′
San Gabriel Mixtepec – 16°05′, 97°06′
San José Lachiquirí – 16°23′, 96°20′
San Juan Acaltepec – 16°16′, 95°56′
San Juan Lachao [Lachao] – 16°14′, 97°09′*
San Juan la Jarcia – 16°31′, 95°56′
San Lucas Ixcotepec – 16°18′, 95°55′*
San Miguel Caja de Agua – 16°09′, 95°23′
San Miguel Suchixtepec – 16°05′, 96°28′
San Pedro Jilotepec – 16°39′, 95°44′
San Vincente – 17°05′, 97°53′
Santa Catalina Quierí – 16°20′, 96°15′*
Santa Cruz Bay – 16°45′, 96°08′*
Santa Efigenia – 16°27′, 94°12′
Santa Lucía – approximately 16°18′, 95°28′
Santa María Candelaria – 16°12′, 95°57′*
Santa María Ecatepec – 16°17′, 95°53′
Santiago Lachiguirí – 16°41′, 95°32′
Santo Domingo – 16°49′, 95°09′
Santo Tomás Ocotepec – 17°08′, 97°46′
Santo Tomás Quierí – 16°21′, 96°10′
Santo Tomás Teipan [Teípam] – 16°15′, 95°58′
Sierra de San Felipe Lachilló – approximately 15°59′, 96°12′
Sierra Juárez – 17°23′, 96°29′*
Sierra Madre [15 mi. N Zanatepec] – approximately 16°41′, 94°21′
Solo de Vega – 16°31′, 96°58′
Tapanatepec – 16°21′, 94°12′
Tehuantepec – 16°21′, 95°14′
Tenango – 16°16′, 95°36′
Teotitlán [del Camino] – 18°08′, 97°05′
Tequisistlán – 16°25′, 95°37′
Tlacolula [de Matamoras] – 16°57′, 96°29′
Tlapancingo [Tlapacingo] – 17°28′, 98°14′
Vincente – 18°31′, 96°31′*
Vista Hermosa – approximately 17°36′, 96°22′
Yaitepec [Santiago Yaitepec] – 16°14′, 97°14′
Yalalag – 17°11′, 96°11′
Zacatepec – 16°46′, 98°00′
Zanatepec – 16°29′, 94°21′
Zapotitlán – 16°08′, 95°43′*
Zarzamora – approximately 16°21′, 95°48′

For additional information on localities in Oaxaca see Duellman (1960:33-35), Rowley (1966:109-112), and Goodwin (1969: 256-265).

Puebla

Acatlán – 18°12′, 98°03′
Amolac – 18°03′, 98°23′
Atlixco – 18°54′, 98°26′
Chila – 18°07′, 98°29′
Izúcar de Matamoros – 18°36′, 98°28′
Metlaltoyuca – 20°44′, 97°51′
Pahuatlán – 20°17′, 98°09′
Piaxtla – 18°12′, 98°15′
Puebla [de Zaragoza] – 19°03′, 98°12′
San Martín [San Martín Texmelucan] – 19°17′, 98°26′
Tehuacán – 18°27′, 97°23′
Tehuitzingo – 18°21′, 98°17′
Tepanco – 18°34′, 97°33′
Tilapa – 18°35′, 98°33′
Totimehuacán [San Francisco Totimehuacán] – 18°58′, 98°11′
Zihuateutla – 20°16′, 97°53′

Querétaro

Amoles [Pinal de Amoles] – 21°09′, 99°39′
Cadereyta [de Montes] – 20°42′, 99°49′
Jalpan – 21°14′, 99°29′
Pinal de Amoles – see Amoles
Querétaro – 20°36′, 100°23′
Tequisquiapan [Tequisquiapam] – 20°31′, 99°52′
Tolimán – 20°55′, 99°56′

Quintana Roo

Felipe Carrillo Puerto – 19°35′, 88°03′
Pueblo Nuevo X-can – 20°50′, 87°43′
Santo Rosa – 19°57′, 88°23′*

San Luis Potosí

Ahualulco – 22°24′, 101°10′
Ajinche – approximately 22°09′, 98°25′
Alvarez – 22°03′, 100°37′
Apetsco – approximately 21°24′, 99°02′
Arriaga – 21°54′, 101°23′
Axtla – approximately 21°28′, 98°51′
Bledos – 21°51′, 101°07′
Cerro Campanario – 21°54′, 100°25′*
Cerro Peñon Blanco – 22°33′, 101°39′*
Ciudad del Maíz – 22°24′, 99°36′
Ciudad Valles [Valles] – 21°59′, 99°01′
Ebano – 22°13′, 98°24′
El Abra – 21°58′, 98°56′
El Bañito – not exactly located, but probably in the vicinity of Ciudad Valles (information supplied by Joseph C. Moore)
El Naranjo [Naranjos] – 22°31′, 99°20′
El Sabinito – approximately 22°31′, 99°22′
El Salto – 22°36′, 99°24′*
Hacienda Angostura – not definitely identified, but may be small railroad station 33 km. NNE Río Verde at 22°14′, 100° 04′
Hacienda Capulín – approximately 21°30′, 99°37′
Hacienda La Parada – 22°21′, 101°13′
Huichihuayán – 21°30′, 98°57′
Jesús María – 21°55′, 100°54′
Paso de San Antonio – 22°01′, 100°24′
Platanito – approximately 22°30′, 99°27′
Puerto de Lobos – approximately 22°29′, 99°34′
Ramos – 22°50′, 101°55′
Río Verde [Ríoverde] – 21°56′, 99°59′
San Carlos – 23°01′, 100°21′
San Luis Potosí – 22°09′. 100°59′
Santa María del Río – 21°48′. 100°45′
Tamazunchale – 21°16′, 98°47′
Tamuín – 21°59′, 98°45′
Taninul – 21°58′, 98°54′
Valles – see Ciudad Valles
Villar – 22°33′, 100°29′

For additional information on localities in San Luis Potosí see Dalquest (1953:215-223).

Sinaloa

Agua Nueva – 24°45′, 107°14′
Badiraguato – 25°22′, 107°31′
Camino Real – 23°52′, 106°39′
Chele – 23°13′, 105°53′
Choix – 26°43′, 108°17′
Comanito – 25°08′, 107°39′
Concepción [La Concha] – 22°32′, 105°28′
Copala – 23°23′, 105°56′
Cosalá – 24°23′, 106°41′
Costa Rica – 24°35′, 107°25′*
Culiacán – 24°48′, 107°24′
Culiacancito – 24°50′, 107°32′
El Cajón – 23°21′, 106°02′
El Dorado – 24°22′, 107°19
El Fuerte – 26°25′, 108°39′
Elota – 23°58′, 106°42′
Esquinapa – 22°50′, 105°46′*
Guamúchil – 25°28′, 108°06′
Guasave – 25°34′, 108°27′
Isla Palmito de Verde – 22°40′, 105°50′
Isla Palmito de la Virgin – 23°00′, 106°10′
Km. marker 1206 on Mexican Highway 15 – not exactly located, but in vicinity of Mazatlán
La Concha – see Concepción
La Cruz – 23°55′, 106°54′
Matatán – 23°02′, 105fiw45′
Mazatlán – 23°13′, 106°25′
Pánuco – 23°25′, 105°55′
Pericos – 25°03′, 107°42′
Piaxtla – 23°52′, 106°39′
Plomosas – 23°04′, 105°29′
Presa Sanalona – 24°48′, 107°09′*
Rosario – 23°00′, 105°52′
San Ignacio – 23°55′, 106°25′
San Juan – 23°51′, 106°20′
Santa Lucía – 23°26′, 106°51′*
Sierra de Choix – approximately 26°50′, 108°11′ (this locality is approximately 15 mi. NE Choix instead of 50 mi. NE Choix as stated on the specimen labels, according to Goldman, 1951:251)
Sinaloa – 25°50′, 108°14′
Teacapán – 22°33′, 105°45′

Vaca – 26°48′, 108°25′
Villa Unión – 23°12′, 106°14′

For additional information about localities in Sinaloa see Hardy and McDiarmid (1969:221-225).

Sonora

Alamos – 27°01′, 108°56′
Camoa – 27°13′, 109°17′
Chinobampo – 26°59′, 109°18′
El Novillo – 28°57′, 109°39′*
Guirocoba – 26°54′, 108°42′*
Hermosillo – 29°04′, 110°58′
Matape – 29°08′, 109°58′
Nácori [Grande] – 29°04′, 110°03′
Nogales – 31°20′, 110°56′
Río Alamos – approximately 26°55′, 109° 09′ (according to R. J. Baker, who collected the specimens, this locality is 11 mi. by road from Alamos in a more or less SSW direction)
Río Cuchajaqui – approximately 26°54′, 108°57′ (according to R. J. Baker, who collected the specimens, this locality is 8 mi. S Alamos)
Tecoripa – 28°37′, 109°57′
Tesia – 27°10′, 109°23′
Ures – 29°26′, 110°24′

For additional information about localities in Sonora see Burt (1938:map 26).

Tamaulipas

Acuña – 23°12′, 98°26′
Altamira – 22°24′, 97°55′
Antiguo Morelos – 22°33′, 99°05′
Aserradero del Paraíso – 22°59′, 99°15′*
Bagdad – 25°57′, 97°09′
Ciudad Mante [El Mante] – 22°44′, 98°57′
Ciudad Victoria [Victoria] – 23°44′, 99°08′
Cruillas – 24°45′, 98°31′
Cueva del Abra – approximately 22°37′, 99°02′ (10 km. NNE Antiguo Morelos)
Ejido Santa Isabel – approximately 23°14′, 99°00′
El Barretal – 24°05′, 99°16′*
El Carrizo – 23°15′, 99°07′
El Encino – approximately 23°08′, 99°07′
El Limón – 22°50′, 99°00′
Gómez Farías – 23°03′, 99°09′
Hacienda Santa Engracia – approximately 24°01′, 99°12′
Hidalgo – 24°15′, 99°26′
Jaumave – 23°25′, 99°23′
La Pesca – 23°46′, 97°47′
La Purísima – 24°17′, 99°28′
Marmolejo – 24°38′, 99°01′
Matamoros – 25°53′, 97°30′
Mesa de Llera – approximately 23°20′, 99° 01′ (see Hooper, 1953:3, for additional information about this locality)
Miquihuana – 23°34′, 99°47′
Mulato [El] – 24°53′, 98°56′
Nicolás – 23°21′, 100°04′*
Padilla – 24°01′, 98°47′
Palmillas – 23°18′, 99°33′
Pano Ayuctle – approximately 23°06′, 99° 07′
Piedra – 23°29′, 98°06′
Quintero – 22°41′, 99°02′
Reynosa – 26°07′, 98°18′
San Fernando – 24°51′, 98°10′
San José – 24°42′, 99°04′
Soto la Marina – 23°46′, 98°13′
Tampico – 22°13′, 97°51′
Tula – 23°00′, 99°43′
Victoria – see Ciudad Victoria
Villa Mainero – 24°34′, 99°36′*

For additional information on localities in Tamaulipas see Alvarez (1963:386-387).

Tlaxcala

Tlaxcala [de Xicohténcatl] – 19°19′, 98°14′

Veracruz

Achotal – 17°44′, 95°10′
Acultzingo – 18°43′, 97°19′
Alvarado – 18°46′, 95°46′
Boca del Río – 19°06′, 96°06′
Carrizal – 19°21′, 96°38′
Catemaco – 18°25′ 95°07′
Cerro Gordo – approximately 19°25′, 96° 40′
Coatzacoalcos – 18°09′, 94°25′
Coyutla – 20°15′, 97°39′
El Tajín – 20°27′, 97°23′
Gutiérrez Zamora – 20°27′, 97°05′
Ixcatepec – 21°13′, 98°00′
Jacales – 20°25′, 98°27′
Jimba – 17°56′, 95°24′
Lago Catemaco – 18°25′, 95°05′
La Mar – 21°32′, 97°40′
Miahuapan [Miahuapa or Miahuapam] – 20°37′, 97°37′
Nautla – 20°13′, 96°47′
Orizaba – 18°51′, 97°05′
Otatitlán – 18°12′, 96°02′
Ozuluama – 21°40′, 97°51′

Papantla – 20°27′, 97°19′
Paraje Nuevo – approximately 18°52′, 96° 52′
Pasa Nueva – approximately 17°59′, 95°11′ (see discussion of this locality in Hall and Dalquest, 1963:184)
Paso de San Juan – 19°12′, 96°19′
Piedras Clavados – approximately 21°11′, 97°59′
Piedras Negras – 18°46′, 96°11′
Plan del Río – approximately 19°23′, 96°36′
Platón Sánchez – 21°17′, 98°22′
Potrero Llano [Potrero del Llano] – approximately 21°10′, 97°43′
Presidio – approximately 18°39′, 96°46′
Puente Nacional – 19°20′, 96°26′
San Andrés Tuxtla – 18°27′, 95°13′
San Carlos [Ursulo Galván] – 19°24′, 96° 21′
San Juan de la Punta [Cuitláhuac] – 18°49′, 96°43′
San Marcos – 20°12′, 96°57′
Santa María – approximately 19°19′, 96°35′, (this is a village at 1800 ft. near the river of the same name, in the lowlands about 20 mi. NE Mirador, according to Goldman, 1951:281)
Santiago Tuxtla – 18°28′, 95°18′
Tihuatlán – 20°43′, 97°32′
Tlapacoyan – 19°58′, 97°13′
Tuxpan – 20°57′, 97°24′
Veracruz – 19°12′, 96°08′

For additional information on localities in Veracruz see Hall and Dalquest (1963: 180-186).

Yucatán

Chichén Itzá – 20°40′, 88°34′
Peto – 20°08′, 88°55′
Pisté – 20°42′, 88°35′
Tizimín – 21°09′, 88°09′

Zacatecas

Berriozábal – 22°33′, 102°19′
Chalchihuites – 23°29′, 103°53′
Hacienda San Juan Capistrano – 22°37′, 104°05′
Jalpa – 21°38′, 102°58′
Moyahua – 21°16′, 103°10′
Noria de Angeles – 22°26′, 101°54′
Rancho Grande – 23°27′, 102°58′
Río Grande – 23°50′, 103°02′
Saín Alto – 23°35′, 103°15′
Santa Rosa – 21°13′, 103°09′
Trancoso – 22°44′, 102°22′
Valparaíso – 22°46′, 103°34′
Zacatecas – 22°47′, 102°35′

NICARAGUA

Alta Gracia, Isla de Ometepe, Rivas – 11° 34′, 85°35′
Boaco, Boaco – 12°27′, 85°43′
Bonanza, Zelaya – 13°57′, 84°32′
Condega, Estelí – 13°21′, 86°25′
Cosigüina, Chinandega – 12°55′, 87°30′
Darailí, Estelí – 13°24′, 86°16′ (this finca is 5 km. N, 14 km. E Condega)*
Dario, Matagalpa – 12°42′, 86°08′
Diriamba, Carazo – 11°53′, 86°15′
El Crucero, Managua – 12°00′, 86°19′
Esquipulas, Matagalpa – 12°37′, 85°49′
Estelí, Estelí – 13°05′, 86°23′
Finca Amayo [Hacienda Amayo], Rivas – 11°19′, 85°43′ (this finca is 13 km. S, 14 km. E Rivas)*
Hacienda Azacualpa, Managua – 12°02′, 86°32′ (this hacienda is 5 km. N, 2 km. W Villa El Carmen)*
Hacienda Bellavista, Volcán Casita, Chinandega – 12°41′, 86°58′
Hacienda Corpus Christi, Managua – 12°16′, 86°23′ (this hacienda is 8 km. NE Mateare)*
Hacienda Cutirre, Volcán Mombacho, Granada – 11°50′, 85°56′ (this hacienda is 11 km. S, 3 km. E Granada)*
Hacienda Mecatepe, Granada – 11°46′, 85° 57′ (this hacienda is 2 km. N, 11½ km. E Nandaime)*
Hacienda Tepeyac, Mataglapa – 13°11′, 85° 56′, (this hacienda is 10½ km. N, 9 km. E Mataglapa)*
Isla Zapatera, Granada – 11°45′, 85°50′
Jinotega, Jinotega – 13°06′, 86°00′
La Calera, Granada – 11°44′, 86°06′ (this hacienda is 3 km. S, 5 km. E Nandaime)*
Lake Jiloa, Managua – 12°13′, 86°19′
Las Maderas, Managua – 12°28′, 86°03′
León, León – 12°26′, 86°54′
Managua, Managua – 12°09′, 86°17′
Masachapa, Managua – 11°47′, 86°31′
Matagalpa, Matagalpa – 12°53′, 85°57′
Mérida, Isla de Ometepe, Rivas – 11°26′, 85°33′
Moyogalpa, Isla de Ometepe, Rivas – 11° 32′, 85°42′

Poneloya, León – 12°22′, 87°02′
Puerto Momotombo, León – 12°24′, 86°37′
Quilalí, Nueva Segovia – 13°32′, 86°00′
Rivas, Rivas – 11°26′, 85°51′
Sabana Grande, Managua – 12°07′, 86°10′
San Antonio, Chinandega – 12°32′, 87°03′
San Pablo, Rivas – 11°36′, 85°57′
San Ramón, Matagalpa – 12°53′, 85°49′
Santa María de Ostuma, Matagalpa – 12° 57′, 85°58′
Sapoá, Rivas – 11°15′, 85°38′
Savala, Matagalpa – approximately 13°03′, 85°31′ (this locality is 45 km. ENE Matagalpa, according to Buchanan and Howell, 1965:549)
Sébaco, Matagalpa – 12°51′, 86°0(′
Tamarindo, León – 12°12′, 86°46′
Uluse [Uluce], Matagalpa – 12°53 85°37′
Villa Somoza, Chontales – 12°08′, 84°58′
Volcán de Chinandega [Volcán San Cristóbal], Chinandega – 12°43′, 87°03′

Panama and Canal Zone

Albrook Air Force Base, Canal Zone – 8°59′, 79733′
Balboa, Canal Zone – 8°57′, 79°34′
Buenos Aires, Panamá – 9°10′, 79°37′
Cacao Plantation, Canal Zone – 9°06′, 79° 41′
Cerro Azul, Panamá – approximately 9°14′, 79°21′
Chepo, Panamá – 9°10′, 79°06′
Chiva Chiva, Canal Zone – 9°02′, 79°35′
Cocoli, Canal Zone – 8°59′, 79°35′
Corte Culebra Road, Canal Zone – coordinates not given by Fairchild and Handley (1966:14)
Curundu, Canal Zone – 8°59′, 79°33′
Empire, Canal Zone – 9°04′, 79°40′ (this is the old administrative center of the canal, located on west bank about halfway between Paraíso and Gamboa)
Farfan, Canal Zone – 8°56′, 79°35′
Fort Clayton, Canal Zone – 8°59′, 79°36′
Fort Kobbe, Canal Zone – 8°55′, 79°35′
Guabalá, Chiriqui – 8°13′, 81°44′
Guánico [Guánico Arriba and Las Palmitas], Los Santos – 7°18′, 80°26′
Juan Mina, Canal Zone – 9°10′, 79°39′
Madden Forest, Canal Zone – 9°06′, 79°37′
Madden Road, Canal Zone – C-25 Road, extending from Paraíso to Madden Dam, passing through Madden Forest
Montijo Bay, Veraguas – near Paracoté (see Aldrich and Bole, 1937:7-8)
Nuevo Emperado, Canal Zone – 9°00′, 79° 44′
Paracoté, Veraguas – approximately 7°40′, 81°00′ (see Aldrich and Bole, 1937:7-8, for additional information about this locality)
Pueblo Nuevo, Panamá – 9°01′, 79°31′
Río Chágres, Canal Zone – 9°08′, 79°41′
Río Hato, Cocle – 8°23′, 80°10′
Rodman Naval Ammunition Depot, Canal Zone – approximately 8°57′, 79°37′ (8 km. W Balboa, according to Fleming, 1970:473; 1971:7)
San Francisco, Veraguas – 8°15′, 80°58′
Santa Fé, Veraguas – 8°31′, 81°05′
Summit, Canal Zone – 9°04′, 79°39′
Tolé, Chiriqui – 8°14′, 81°41′

For additional information on localities in Panamá and the Canal Zone see Goldman (1920:4-18) and Fairchild and Handley (1966:9-22).

United States

Texas

Alamo, Hidalgo County – 26°11′, 98°07′
Bayside, Cameron County – not exactly located, but approximately 26°07′, 97°!5′
Bentsen State Park, Hidalgo County – approximately 26°10′, 98°21′ (4 mi. SW Mission)
Brownsville, Cameron County – 25°54′, 97°30′
Edinburg, Hidalgo County – 26°19′, 98°09′
Elsa, Hidalgo County – 26°18′, 97°59′
Fort Brown, Cameron County – 25°54′, 97°30′
Ingram, Kerr County – 30°05′, 99°14′
Lomita Ranch, Hidalgo County – approximately 26°10′, 98°22′ (based on information in files of U.S. Biological Survey, Washington, D.C.)
McAllen, Hidalgo County – 26°11′, 98°14′
Mission, Hidalgo County – 26°12′, 98°19′
Raymondville, Willacy County – 26°29′, 97°46′
Rio Hondo, Cameron County – 26°15′, 97° 35′
San Benito, Cameron County – 26°08′, 97° 37′

All localities in Texas were plotted from the Monterrey quadrat (NG-14) of the

American Geographical Society's "Map of Hispanic America. . . ." For additional information on localities in Texas see Blair (1952:231-232).

VENEZUELA

Agua Santa, Trujillo – 9°32′, 70°38′*
Carúpano, Sucre – 10°40′, 63°14′*
Maracaibo, Zulia – 10°40′, 71°37′*
Rancho Grande, Aragua – 10°22′, 67°41′*
Valera, Trujillo – 9°19′, 70°37′*

APPENDIX II

Ectoparasites known from *Liomys* and *Heteromys* are listed below. Numbers in source column indicate unpublished records from the files of the following specialists: Richard B. Loomis (Trombiculidae); Russell W. Strandtmann (Laelapidae); Burruss McDanial (Listrophoridae); John B. Kethley (Cheyletidae); Glen M. Kohls and Eleanor K. Jones (Ixodides); K. C. Emerson (Anoplura); Robert Traub (Siphonaptera). Localities of collection corresponding to each number are listed following the list of ectoparasites.

Ectoparasite		
Family	Species	Source
	Liomys irroratus	
Trombiculidae	*Ectonyx fusicornis*	Brennan (1960*a*:88); 6
"	*Euschoengastia gagarini*	Brennan (1962:618)
"	*Euschoengastoides bigenuala*	Loomis and Crossley (1963:379); Eads *et al.* (1965:17)
"	*Euschoengastoides lacerta*	Loomis and Crossley (1963:380); Eads *et al.* (1965:17)
"	*Euschoengastoides loomisi*	Loomis and Crossley (1963:380); Eads *et al.* (1965:17)
	Eutrombicula alfreddugesi	Eads *et al.* (1965:17)
"	*Fonsecia* (*Parasecia*) *universitatis*	Hoffmann (1963:108); Brennan (1969:666)
"	*Hexidionis allredi*	Eads *et al.* (1965:17)
"	*Hexidionis jessiemae*	Brennan (1965:83)
"	*Leptotrombidium panamense*	Loomis and Crossley (1963:378); Eads *et al.* (1965:17)
"	*Odontacarus cayolargoensis*	Loomis and Crossley (1963:381); Eads *et al.* (1965:17)
"	*Pseudoschoengastia audyi*	Brennan and Dalmat (1960:191); Eads *et al.* (1965:17)
"	*Pseudoschoengastia farneri*	Loomis and Crossley (1963:381); Eads *et al.* (1965:17)
"	*Pseudoschoengastia hoffmannae*	5
"	*Pseudoschoengastia hungerfordi*	5, 6
"	*Trombicula bakeri*	8
"	*Trombicula* n. sp.	Eads *et al.* (1965:17)
"	*Xenacarus plumosus*	Loomis and Crossley (1963:382); Eads *et al.* (1965:17)
Laelapidae	*Androlaelaps fahrenholzi*	Eads *et al.* (1965:17)

"	*Hirstionyssus neotomae*	Eads *et al.* (1965:17)
"	*Hirstionyssus* n. sp.	Eads *et al.* (1965:17)
"	*Steptolaelaps liomydis*	Grant (1947:8); Furman (1955:525); Eads *et al.* (1965:17)
Macronyssidae	*Ornithonyssus bacoti*	Eads *et al.* (1965:17)
"	*Ornithonyssus sylvarium*	Eads *et al.* (1965:17)
Listrophoridae	*Listrophorus* n. sp.	Eads *et al.* (1965:17)
Argasidae	*Ornithodoros talaje*	Eads *et al.* (1965:17)
Ixodidae	*Ixodes eadsi*	Kohls and Clifford (1964:466); Eads *et al.* (1965:17)
Hoplopleuridae	*Fahrenholzia ehrlichi*	Ferris (1922:161); Johnson (1962:417); Eads *et al.* (1965:17); Emerson (1971*b*: 374)
"	*Fahrenholzia texana*	Ferris (1922:161); Stojanovich and Pratt (1961:693); Johnson (1962:426); Eads *et al.* (1965:17)
Pulicidae	*Hoplopsyllus* (*Euhoplopsyllus*) *glacialis*	10
Rhopalopsyllidae	*Polygenis gwyni*	Eads and Menzies (1949:37); Eads (1950:62); 1, 2
"	*Polygenis martinezbaezi*	2, 3, 4, 7, 9

Liomys pictus

Trombiculidae	*Anahuacia*	41
"	*Ectonyx fusicornis*	8, 13, 14, 18, 20, 21, 22, 25, 26, 27, 36
"	*Euschoengastia gagarini*	26, 28
"	*Euschoengastoides arizonae*	Loomis (1971:699); 1
"	*Euschoengastoides expansellus*	Loomis (1971:700); 8
"	*Euschoengastoides tumidus*	Loomis (1971:703); 7, 8, 27, 31
"	*Eutrombicula alfreddugesi*	41
"	*Eutrombicula* sp.	28
"	*Fonsecia* (*Parasecia*) sp.	25, 26, 28, 37
"	*Hexidionis allredi*	2, 6
"	*Leptotrombidium panamense potosinum*	2, 3, 4, 8, 9, 10, 19, 20, 21, 22, 24, 26, 28, 37, 41
"	*Leptotrombidium* n. sp. "c"	8, 11, 12, 15, 16, 20, 21, 22, 23, 24, 25, 26, 29
"	*Neotrombicula* sp.	20, 24
"	*Odontacarus* sp.	3, 28
"	*Otorhinophila intrasola*	Wrenn and Loomis (1967:160); 3, 9
"	*Otorhinophila sinaloae*	Wrenn and Loomis (1967:164); 8

"	*Pseudoschoengastia aberrans*	38
"	*Pseudoschoengastia audyi*	Brennan and Dalmat (1960:191)
"	*Pseudoschoengastia guatemalensis*	Brennan and Dalmat (1960:191)
"	*Pseudoschoengastia hoffmannae*	Brennan (1960 *b*: 486), 34
"	*Pseudoschoengastia hungerfordi*	13, 33, 34, 37
"	*Pseudoschoengastia scitula*	Brennan and Jones (1959:427)
"	*Pseudoschoengastia* n. sp. "e"	20
"	*Pseudoschoengastia* n. sp. "j"	20, 24, 25, 26, 28, 29
"	*Pseudoschoengastia* sp.	41
"	*Sasacarus whartoni*	26
Laelapidae	*Androlaelaps leviculus*	11
"	*Steptolaelaps heteromys*	14, 41
"	*Steptolaelaps liomydis*	Furman (1955:525); 11, 14, 17, 18, 41
Ixodidae	*Ixodes sinaloa*	Kohls and Clifford (1966:811, 813); Keirans and Jones (1972:474)
"	*Ixodes* sp.	11, 14
Hoplopleuridae	*Fahrenholzia microcephala*	Ferris (1922:161); Johnson (1962:416); Emerson (1971*b*:375); 11, 14, 17, 18, 37, 41
Ceratophyllidae	*Jellisonia wisemani*	13, 14
Rhopalopsyllidae	*Polygenis gwyni*	32
"	*Polygenis martinezbaezi*	4, 30, 35
"	*Polygenis vazquezi*	Hubbard (1958:165)
"	*Polygenis vulcanius*	38, 39, 40, 41
"	*Polygenis* sp.	5

Liomys salvini

Trombiculidae	*Anahuacia* n. sp. "t"	19, 21, 23
"	*Ascoschoengastia dyscrita*	19
"	*Cordiseta mexicana*	6, 9, 18, 20, 21, 23
"	*Euschoengastia* sp.	15
"	*Euschoengastoides* sp.	6
"	*Eutrombicula alfreddugesi*	3, 6, 9, 11, 12, 17, 20, 21, 22, 23
"	*Fonsecia* (*Parasecia*) sp.	7, 9
"	*Leptotrombidium panamense panamense*	6, 7, 15, 19, 20
"	*Leptotrombidium panamense potosinum*	1
"	*Microtrombicula perplexa*	Webb and Loomis (1971:5)
"	*Pseudoschoengastia costaricensis*	Geest and Loomis (1968:38, 40)
"	*Pseudoschoengastia guanacastensis*	Geest and Loomis (1968:36, 38)
"	*Pseudoschoengastia hoguei*	Geest and Loomis (1968:25, 28)

"	*Pseudoschoengastia* sp.	6, 7, 9, 11, 15, 17
"	*Trombicula dunni*	9
Laelapidae	*Androlaelaps fenilis*	7, 12
"	*Eubrachylaelaps ? circularis*	7
"	*Hirstionyssus galindoi*	7
"	*Hypoaspis lubrica*	7
"	*Hypoaspis* sp.	7
"	*Steptolaelaps heteromys*	7, 8, 9, 10, 11, 12, 13, 14, 16, 17
Listrophoridae	*Listrophorus* sp.	11
Cheyletidae	*Eucheyletia* n. sp.	7
Ixodidae	*Amblyomma* sp.	4
"	*Ixodes eadsi* (or near)	9, 11
"	*Ixodes sinaloa*	Keirans and Jones (1972:474)
Hoplopleuridae	*Fahrenholzia fairchildi*	Johnson (1962:419); Emerson (1971*a*: 333)
Rhopalopsyllidae	*Polygenis vulcanius*	2, 5, 24
	Liomys adspersus	
Trombiculidae	*Ascoschoengastia dyscrita*	Brennan and Jones (1961:107); Brennan and Yunker (1966:227)
"	*Colicus liomys*	Brennan and Jones (1961:121); Brennan and Yunker (1966:254)
"	*Crotonasis fissa*	Brennan and Yunker (1966:231)
"	*Eutrombicula goeldii*	Brennan and Yunker (1966:236)
"	*Leptotrombidium panamense panamense*	Brennan and Yunker (1966:238)
"	*Odontacarus fieldi*	Brennan and Yunker (1966:224)
"	*Polylopadium kramisi*	Brennan and Jones (1961:112); Brennan and Yunker (1966:243)
"	*Pseudoschoengastia bulbifera*	Brennan (1960 *b*:483); Brennan and Yunker (1966:245)
"	*Pseudoschoengastia tricosa*	Brennan and Jones (1961:123); Brennan and Yunker (1966:257)
"	*Pseudoschoengastia zona*	Brennan (1960*b*:490); Brennan and Yunker (1966:248); Geest and Loomis (1968:25)
Laelapidae	*Androlaelaps fahrenholzi*	Tipton *et al.* (1966:34)
"	*Hirstionyssus microchelae*	Strandtmann and Yunker (1966:114)
"	*Steptolaelaps heteromys*	Tipton *et al.* (1966:39)
Macronyssidae	*Ornithonyssus bacoti*	Yunker and Radovsky (1966:89)
Ixodidae	*Amblyomma* sp.	Fairchild *et al.* (1966:211)

Hoplopleuridae	*Fahrenholzia fairchildi*	Johnson (1962:419); Wenzel and Johnson (1966:275)
Pulicidae	*Ctenocephalides felis felis*	Tipton and Méndez (1966:292)
Rhopalopsyllidae	*Polygenis dunni*	Tipton and Méndez (1966:298)
"	*Polygenis klagesi*	Tipton and Méndez (1966:298)

Liomys sp.

Ceratophyllidae	*Jellisonia hayesi*	3
Rhopalopsyllidae	*Polygenis gwyni*	2
"	*Polygenis martinezbaezi*	1

Heteromys anomalus

Trombiculidae	*Acomatacarus tubercularis*	Brennan (1952:146)
"	*Anomalaspis ambiguus*	Brennan (1952:146)
"	*Colicus flochi*	Brennan and Jones (1960:504)
"	*Crotiscus desdentatus*	Brennan (1957:675)
"	*Eutrombicula alfreddugesi*	Brennan and Jones (1960:506)
"	*Eutrombicula goeldii*	Brennan and Jones (1960:508)
"	*Fonsecia (Parasecia) manueli*	Brennan and Jones (1960:520)
"	*Kymocta faitkeni*	Brennan (1968*a*:614); Brennan and Yunker (1969:304)
Laelapidae	*Androlaelaps fahrenholzi*	Furman and Tipton (1961:185)
"	*Echinolaelaps boultoni*	Furman and Tipton (1961:170)
"	*Eubrachylaelaps rotundus*	Furman and Tipton (1961:171)
"	*Gigantolaelaps wolffsohni*	Furman and Tipton (1961:179)
"	*Mysolaelaps parvispinosus*	Furman and Tipton (1961:195)
"	*Steptolaelaps heteromys*	Fox (1947:119); Furman (1955:521); Furman and Tipton (1961:195)
Glycyphagidae	*Dermacarus ornatus*	Fain (1967:425)
Ixodidae	*Amblyomma ovale*	1
"	*Amblyomma* sp.	2, 3
"	*Ixodes venezuelensis*	Kohls (1953:301); Vogelsang and Santos Dias (1953:67)
Hoplopleuridae	*Fahrenholzia schwartzi*	Werneck (1952:70); Johnson (1962:418)

Rhopalopsyllidae	*Polygenis bohlsi bohlsi*	Traub and Johnson (1952:128); Johnson (1957:160); Cova Garcia and Tallaferro D. (1959:346)
"	*Polygenis bohlsi jordani*	Cova Garcia and Tallaferro D. (1959: 346)
"	*Polygenis dunni*	Johnson (1957:160)
"	*Polygenis peronis*	Jordan and Rothschild (1923:343); Costa Lima and Hathaway (1946:144); Fox (1947:117); Traub and Johnson (1952:128); Johnson (1957:166); Cova Garcia and Tallaferro D. (1959: 346)
"	*Polygenis roberti beebei*	Traub and Johnson (1952:127); Johnson (1957:169); Cova Garcia and Tallaferro D. (1959:347)
"	*Polygenis* sp.	Traub and Johnson (1952:131)

Heteromys australis

Trombiculidae	*Eutrombicula goeldii*	Brennan and Yunker (1966:236)
"	*Polylopadium tertium*	Brennan (1968*b*:679)
"	*Pseudoschoengastia bulbifera*	Brennan and Yunker (1966:245)
"	*Pseudoschoengastia zona*	Brennan and Yunker (1966:248)
"	*Quadraseta trapidoi*	Brennan (1968*b*:683)
"	*Trombicula almae*	Brennan (1968*b*:683)
"	*Trombicula dunni*	Brennan and Yunker (1966:253); Brennan (1968*b*:684)
"	*Trombicula keenani*	Brennan and Yunker (1966:254)
Laelapidae	*Androlaelaps fahrenholzi*	Tipton *et al.* (1966:34)
"	*Steptolaelaps heteromys*	Tipton *et al.* (1966:39)
Rhopalopsyllidae	*Polygenis klagesi*	Tipton and Méndez (1966:298)

Heteromys desmarestianus

Trombiculidae	*Anahuacia* sp.	1

"	*Ascoschoengastia dyscrita*	Brennan and Yunker (1966:227)
"	*Crotiscus desdentatus*	Brennan and Yunker (1966:229); 3, 4
"	*Euschoengastia belgicae*	Brennan and Yunker (1966:233)
"	*Eutrombicula alfreddugesi*	Brennan and Yunker (1966:235); 3
"	*Eutrombicula goeldii*	Brennan and Yunker (1966:236)
"	*Hoffmannina handleyi*	Brennan and Jones (1961:111); Brennan and Yunker (1966:237); 6
"	*Kymocta teratarsalis*	Yunker and Brennan (1962:574); Brennan and Yunker (1966: 231); Brennan (1968*a*:615)
"	*Leptotrombidium haemaxiaium*	5, 6
"	*Odontacarus* sp.	2
"	*Pseudoschoengastia bulbifera*	Brennan and Yunker (1966:245); 6
"	*Pseudoschoengastia finitima*	Brennan and Yunker (1966:247); Geest and Loomis (1968:33)
"	*Pseudoschoengastia tricosa*	Brennan and Yunker (1966:257)
"	*Sasacarus furmani*	Brennan and Yunker (1966:224); 5
"	*Sasacarus vercammeni*	Brennan and Dalmat (1960:183)
"	*Trombicula dicrura*	Brennan and Jones (1961:118); Brennan and Yunker (1966:253)
"	*Trombicula dunni*	Brennan and Yunker (1966:253)
"	*Trombicula keenani*	Brennan and Yunker (1966:254)
Laelapidae	*Androlaelaps fahrenholzi*	Tipton *et al.* (1966:33)
"	*Eubrachylaelaps jamesoni*	Tipton *et al.* (1966:26)
"	*Hirstionyssus heteromydis*	Strandtmann and Yunker (1966:108)
"	*Hirstionyssus lunatus*	Strandtmann and Yunker (1966:123)
"	*Hirstionyssus microchelae*	Strandtmann and Yunker (1966:116)
"	*Hirstionyssus minutus*	Strandtmann and Yunker (1966:112)
"	*Hirstionyssus panamensis*	Strandtmann and Yunker (1966:110); 1

"	*Steptolaelaps heteromys*	Tipton *et al.* (1966:39); 1
"	*Tur uniscutatus*	Tipton *et al.* (1966:41)
Speleognathidae	*Paraspeleognathopsis cricetidarum*	Clark (1967:241)
Hoplopleuridae	*Fahrenholzia fairchildi*	Johnson (1962:419); Wenzel and Johnson (1966:275)
"	*Fahrenholzia ferrisi*	Johnson (1962:418); Emerson (1971*a*:333); 1
"	*Fahrenholzia hertigi*	Johnson (1962:422); Wenzel and Johnson (1966:275)
Rhopalopsyllidae	*Polygenis roberti beebei*	Tipton and Méndez (1966:299)
Ceratophyllidae	*Kohlsia traubi*	Tipton and Méndez (1966:316)
"	*Pleochaetis dolens dolens*	Tipton and Méndez (1966:311)
Hystrichopsyllidae	*Wenzella obscura*	Traub (1953:78)
"	*Wenzella yunkeri*	Tipton and Méndez (1966:320)

Heteromys gaumeri

Trombiculidae	*Cordiseta mexicana*	Loomis (1969:6)
"	*Ectonyx fusicornis*	Loomis (1969:6)
"	*Fonsecia gurneyi*	Loomis (1969:9)
"	*Leptotrombidium panamense*	Loomis (1969:10)
"	*Odontacarus cayolargoensis*	Loomis (1969:5)
"	*Pseudoschoengastia extrinseca*	Loomis (1969:11)
"	*Pseudoschoengastia scitula*	Loomis (1969:12)
Laelapidae	*Androlaelaps fahrenholzi*	6
"	*Eubrachylaelaps jamesoni*	6
"	*Hypoaspis lubrica*	6
"	*Hypoaspis* sp.	5
"	*Steptolaelaps heteromys*	2, 3, 4, 5, 6
Ixodidae	*Amblyomma* sp.	6
"	*Ixodes* sp.	6
Hoplopleuridae	*Fahrenholzia ferrisi*	Emerson (1971*b*:374); 1, 4, 6

Heteromys goldmani

Hoplopleuridae	*Fahrenholzia ferrisi*	Ferris (1922:161); Werneck (1952:73); Johnson (1962:418); 1

Heteromys sp.

Ixodidae	*Amblyomma* sp.	Fairchild *et al.* (1966:211)
"	*Dermacentor* sp.	Fairchild *et al.* (1966:211)

The localities indicated by numbers in the source column above are identified and listed below by host species.

Liomys irroratus

NUEVO LEON: (1) El Potosi. DURANGO: (2) 5 1/2 mi. NNW Canatlán; (3) 3 mi. NNW Canatlán. JALISCO: (4) Lagos de Moreno; (5) 2 6/10 mi. E Etzatlán; (6) Nevado de Colima. MICHOACAN: (7) 8 mi. NE Pátzcuaro; (8) 4 mi. NE Pátzcuaro, (9) 5 mi. S Pátzuaro. OAXACA: (10) Monte Alban.

Liomys pictus

SONORA: (1) 8 mi. W Alamos; (2) 8 mi. SE Alamos; (3) 7.7 mi. SSE Alamos; (4) 8 mi. SSE Alamos; (5) 9 mi. S Alamos. SINALOA: (6) 4.7 mi. SW San Blas; (7) 25 km. N, 1 km. E Culiacán; (8) 14 mi. N, 0.2 mi. W Culiacán; (9) 14 mi. N Culiacán; (10) 3 mi. E Culiacancito; (11) 5 km. SW San Ignacio; (12) 1 mi. W Mexican Highway 15 along Río Piaxtla; (13) 1.2 mi. NE Santa Lucía; (14) 1 km. NE Santa Lucía; (15) 1 mi. E Panuco; (16) 26 mi. NE Villa Unión; (17) 7.3 km. SW Matatan. NAYARIT: (18) 1 1/2 km. N San Miguel; (19) 21 mi. S Acaponeta; (20) 8.7 mi. NE San Blas; (21) 2.6 mi. E San Blas; (22) 3.4 mi. E San Blas; (23) 4 mi. E San Blas; (24) 7 km. E San Blas; (25) 5 mi. E San Blas; (26) 9 km. E San Blas; (27) 8.8 mi. E San Blas; (28) 1 km. S, 14 km. E San Blas; (29) 5 mi. SE San Blas; (30) 1 mi. W Tepic; (31) 0.5 mi. W Jalisco. JALISCO: (32) 6 mi. W San Marcos; (33) 4 km. NE Contla; (34) 20 km. WNW Purificación; (35) 3.5 mi. WNW Zapoltitic; (36) 11 mi. SW Autlán; (37) 4 km. W Tuxpan. CHIAPAS: (38) 11 km. NNW Tuxtla; (39) Cerro del Cañon del Siamidera, 4 km. N Tuxtla; (40) 4 mi. E Tuxtla; (41) Finca San Salvador, 15 km. SE San Clemente.

Liomys salvini

CHIAPAS: (1) 16 km. SE Tapachula. GUATEMALA: (2) 11 mi. SW Escuintla. NICARAGUA: (3) Darailí, 5 km. N, 14 km. E Condega; (4) 4 1/2 km. N Cosigüina; (5) La Danta, 1 km. N, 5 km. E Esquipulas; (6) 1 km. NE Esquipulas; (7) Hda. Bellavista, Volcán Casita; (8) San Antonio; (9) Santa Rosa, 17 km. N, 15 km. E Boaco; (10) 8 km. (by road) N Las Maderas; (11) 1 km. N, 2 1/2 km. W Villa Somoza; (12) 3 km. N, 4 km W Diriamba; (13) Moyogalpa, NW end Isla de Ometepe; (14) 6 km. E Moyogalpa, NW end Isla de Ometepe; (15) 2 km. N, 3 km. E Mérida; (16) Finca Amayo, 13 km. S, 14 km. E Rivas; (17) Río Javillo, 4 km. W Sapoá. COSTA RICA: (18) 9 km. N Liberia; (19) 5 km. N, 4 km. W Liberia; (20) 5 mi. N Liberia; (21) 7.5 km. S Liberia; (22) Playa del Cocos; (23) 3 km. S Playa del Cocos; (24) 5 km. NW Tilarán.

Liomys sp.

JALISCO: (1) Zaputlanedo, 24 mi. S Guadalajara; (2) 5 mi. S Ciudad Guzmán. GUERRERO: (3) Omilteme.

Heteromys anomalus

VENEZUELA: (1) Manacal, 5 km. S, 25 km. E Carúpano, Sucre; (2) Hda. Socopito, 20 km. S, 98 km. E Maracaibo, *in* Falcon; (3) near Agua Santa, 23 km. NW Valera, Trujillo.

Heteromys desmarestianus

CHIAPAS: (1) (Sabena de) San Quintin. NICARAGUA: (2) Santa María de Ostuma. COSTA RICA: (3) 2.9 km. S Puerto Viejo; (4) Río Claro, 16.4 mi. N San José on San Jeronimo Road; (5) Pandora; (6) Monte Verde.

Heteromys gaumeri

YUCATAN: (1) 3 km. N Pisté; (2) 2 km. N Pisté; (3) Pisté. QUINTANA ROO: (4) 4 km. NNE Felipe Carrillo Puerto. CAMPECHE: (5) 5 km. S Champotón; (6) 7.5 km. W Escárcega.

Heteromys goldmani

CHIAPAS: (1) Volcán Tacaná, 8 km. NNE Unión Juárez.

APPENDIX III

Matrices of characters used in analyses of evolutionary relationships of *Liomys* and *Heteromys*. Characters marked with an asterisk are those used in the final analyses. Values given for *Heteromys* in this matrix are based mostly upon *H. desmarestianus*, but some represent *H. lepturus* and *H. gaumeri*. Characters marked NC (no comparison) indicate that no values were available for the species.

Character	*Liomys irroratus*	*Liomys pictus*	*Liomys spectabilis*	*Liomys salvini*	*Liomys adspersus*	*Heteromys* sp.
(1)* Greatest length of skull	33.6	32.0	34.2	31.5	35.5	37.1
(2) Zygomatic breadth	15.9	14.9	15.7	14.7	16.6	16.9
(3) Length of rostrum	15.1	14.3	15.5	13.3	15.7	16.9
(4) Length of hind foot	32.7	28.7	30.5	26.9	30.8	36.0
(5) Zygomatic breadth/Greatest length of skull × 100	46.9	46.6	45.8	46.7	46.8	45.6
(6) Interorbital constriction/ Greatest length of skull × 100	24.2	24.4	23.4	20.5	21.3	26.1
(7) Mastoid breadth/Greatest length of skull × 100	44.6	43.8	42.7	43.8	41.4	42.0
(8) Length of nasals/Greatest length of skull × 100	38.6	39.7	39.9	37.3	40.9	42.0
(9) Length of rostrum/Greatest length of skull × 100	45.0	44.7	45.4	42.2	44.3	45.7
(10) Length of maxillary toothrow/Greatest length of skull × 100	16.0	15.0	15.4	15.1	15.1	14.4
(11) Depth of braincase/ Greatest length of skull × 100	27.1	27.2	24.7	27.1	26.7	25.3
(12) Interparietal width/ Greatest length of skull × 100	25.3	27.8	25.1	28.3	22.2	23.1
(13) Interparietal length/ Greatest length of skull × 100	11.9	14.4	12.9	12.7	12.9	14.3
(14)* Notching on posterior margin of interparietal	2.2	2.0	2.3	2.2	1.3	3.0
(15)* Division of interparietal	1.2	1.2	1.0	1.1	1.2	1.0
(16)* Shape of termination of nassals	2.2	1.4	1.5	1.6	3.0	3.0
(17)* Length of nasals in comparison with premaxillaries	1.0	1.3	1.1	1.0	1.0	1.3
(18)* Wear pattern of molars	2	2	2	3	3	1
(19)* Accessory enamel islands on molars	2	2	2	2	2	1

(20)* Lophids on lower premolars	2	2	2	2	2	3
(21)* Re-entrant angle on labial margin of metalophid	2	2	2	3	3	1
(22)* Separation of entostyle on upper premolar	1.4	1.0	1.0	1.6	1.6	2.0
(23)* Length P4/Greatest length of skull × 100	4.88	4.64	4.69	4.59	4.38	4.06
(24) Width P4/Greatest length of skull × 100	5.28	4.91	5.13	4.77	4.68	4.01
(25) Length M1/Greatest length of skull × 100	3.02	2.93	2.98	2.96	2.82	2.78
(26) Width M1/Greatest length of skull × 100	5.19	4.80	5.13	4.48	4.40	3.86
(27)* Sculpturing on glans penis	1.0	2.0	2.0	3.0	3.0	1.0
(28)* Lobes on urethral lappets	3	3	3	2	2	3
(29) Length of glans penis	5.5	5.5	6.3	5.2	6.1	6.8
(30)* Length of glans/Length of baculum × 100	78.5	65.4	64.2	73.5	68.1	79.0
(31)* Length of tip/Length of glans × 100	20.0	28.2	28.6	14.1	18.4	19.9
(32)* Morphology of baculum	1	3	3	2	2	1
(33)* Length of baculum	8.2	8.7	9.5	7.9	9.6	8.8
(34)* Length of baculum/Length of hind foot × 100	27.4	31.0	31.5	28.6	29.2	23.8
(35)* Number of chromosomes	60	48	48	56	56	60
(36)* Fundamental number	62	66	64	86	84	82
(37)* X-chromosome	2	1	1	2	2	2
(38) Y-chromosome	2	1	1	1	1	NC
(39) Length of head of spermatozoa/Width of head of spermatozoa	2.72	2.88	2.69	1.08	1.13	NC
(40) Length of neck of spermatozoa	0.00	0.74	0.62	0.54	0.75	NC
(41) Parasitized by *Fahrenholzia ehrlichi* and *F. texana*	2	1	NC	1	1	1
(42) Parasitized by *Fahrenholzia microcephala*	1	2	NC	1	1	1
(43) Parasitized by *Fahrenholzia fairchildi*	1	1	NC	2	2	2
(44) Parasitized by *Fahrenholzia ferrisi* and *F. hertigi*	1	1	NC	1	1	2
(45)* Shape of interpterygoid fossa	1	1	1	1	1	2
(46)* Plantar tubercles	5	6	6	6	6	6
(47)* Soles of hind feet	1	1	1	1	1	2
(48)* Reproduction	4.4	3.8	5.0	3.6	3.2	3.3
(49)* Ecology	1	1	1	1	1	2
(50)* Lateral stripe	2	2	2	1	1	2
(51)* Dominant wavelength	583.0	583.3	583.8	582.9	581.6	584.3
(52)* Brightness (%)	9.36	9.57	8.54	7.58	7.86	6.56
(53)* Purity (%)	20.86	26.37	27.69	20.58	21.12	20.40

APPENDIX IV

Sources of values and methods for scoring characters in Appendix III were as follows.

Mensural data (characters 1-13).—These data combine values for males and females from the following samples: (1) *Liomys irroratus*—central Oaxaca (samples 15-16); (2) *Liomys pictus*—Isthmus of Tehuantepec, Oaxaca (sample 24); (3) *Liomys spectabilis*—southeastern Jalisco (only known sample); (4) *Liomys salvini*—coastal Chiapas (sample 2); (5) *Liomys adspersus*—vicinity of Canal Zone (sample 1); (6) *Heteromys desmarestianus*—Chiapas, Guatemala, Nicaragua, and Costa Rica (specimens used in section on external and cranial morphology).

Qualitative cranial characters (14-17).—The values for the five species of *Liomys* are based upon all specimens scored for each species and those for *Heteromys desmarestianus* are based upon the same individuals that were used for mensural data. Methods for scoring these characters are explained in the section on Methods, Materials, and Acknowledgments.

Wear pattern of molars (18).—Median valley of enamel persistent into adulthood, 1; median valley of enamel not persistent, but forming an island of enamel on M1 before worn away, 2; median valley of enamel not persistent and not forming, or forming for only a short period, an island of enamel on M1, 3.

Accessory enamel islands on molars (19).—Accessory enamel islands on molars well developed and persistent, 1; accessory enamel islands on molars not well developed and only visible in unworn teeth, 2.

Lophids on lower premolar (20).—All species of *Liomys* have only two lophids, protolophid and metalophid, on the lower premolar whereas species of *Heteromys* have either three or four lophids on lower premolars.

Re-entrant angle on labial margin of metalophid (21).—Absent, 1; present, but not reaching median valley, 2; present and reaching median valley, 3.

Separation of entostyle on upper premolar (22).—Entostyle closely joined to hypocone, 1; entostyle separated from hypocone, 2.

Size of teeth (23-26).—Based on data presented in section on tooth structure.

Sculpturing on glans penis (27).—Weak sculpturing on external surface of glans, crenulation around terminal crater very weakly defined, 1; moderate sculpturing, crenulation around terminal crater distinct but not deeply incised, 2; glans heavily sculptured, crenation on terminal crater deeply incised, 3.

Lobes on urethral lappets (28).—Count of lobes present on lappets.

Mensural data for glans penis (29-31).—Based upon data given in section on morphology of glans penis. All data on glans for *Heteromys* are based upon *Heteromys lepturus.*

Morphology of baculum (32).—Shaft of baculum oval to tip with very small laterally flattened tip, 1; shaft of baculum with dorsoventrally flattened area before upturned tip, 2; shaft of baculum with a laterally compressed ventral keel at tip with a dorsoventrally flattened area posterior to the keel, 3.

Mensural data for bacula (33-34).—Based on data presented in section on bacular morphology.

Karyology (35-36).—Data presented in section on comparative karyology.

X-chromosome (37).—X-chromosome a large metacentric chromosome, 1; X-chromosome a large submetacentric chromosome, 2.

Y-chromosome (38).—Y-chromosome a medium-sized metacentric chromosome, 1; Y-chromosome a medium-sized subtelocentric chromosome, 2.

Morphology of spermatozoa (39-40).—Based upon data presented in section on morphology of spermatozoa.

Ectoparasites (41-44).—Parasites absent, 1; parasites present, 2.

Shape of interpterygoid fossa (45).—Fossa U-shaped, 1; fossa V-shaped, 2.

Plantar tubercles (46).—Counts of number of plantar tubercles found on hind feet.

Soles of hind feet (47).—Soles of hind feet haired, 1; soles of hind feet naked, 2. All members of the genus *Heteromys*, except *H. gaumeri* have naked soles on their hind feet.

Reproduction (48).—Average embryo count or litter size.

Ecology (49).—Inhabiting mainly arid to semiarid areas of scrub thorn forest and grasslands, 1; inhabiting moister areas including rain or cloud forests, 2.

Lateral stripe (50).—Stripe absent, 1; stripe present, 2.

Coloration (51-53).—Based upon data presented in section on pelage.