

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3050, 56 pp., 25 figures, 15 tables July 28, 1992

A Revision of the South American Species of *Sigmodon* (Mammalia: Muridae) with Notes on Their Natural History and Biogeography

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ABSTRACT

Cotton rats, members of the muroid rodent genus *Sigmodon*, range from Iowa and Nebraska to northeastern Brazil and Peru. Seven valid species are currently recognized in North and Central America, but the 12 nominal species known from South America have received no critical taxonomic attention to date. This revision, based on morphological character data from almost 1300 museum specimens, demonstrates the existence of four diagnosable species in the South American fauna. Specimens with ungrooved upper incisors from Colombia and northwestern Venezuela closely resemble typical *hispidus* in all qualitative and quantitative comparisons, including karyotypes, and are provisionally referred to that species. Specimens of *alstoni*, a smaller cotton rat with deeply grooved upper incisors, distinctive craniodental proportions, and very divergent karyotypes, have been found in sympatry with *hispidus* at several localities; this species ranges from extreme northeastern Colombia throughout most of Venezuela, and is also known from scattered localities in Guyana, Surinam, and Brazil north of the Amazon River. A third species, *peruanus*, is restricted to the Pacific lowlands and foothills of western Ecuador and northwestern Peru; it differs from *hispidus* and other congeners in numerous qualitative and quantitative aspects of craniodental morphology including a uniquely primitive pattern of stapedial

arterial supply. Known from only two localities in the high Andes of western Ecuador, *inopinatus* is strikingly divergent from all other South American species in rostral and interorbital morphology.

Available natural history information suggests that South American species of *Sigmodon*, like their North American congeners, inhabit nonforest environments, are active both by day and at night, construct runways, and chiefly consume the green leaves and stems of grasses and forbs. Comparisons with sympatric species of *Zygodontomys* and *Holochilus* suggest that cotton rats are the only strictly terrestrial (nonaquatic and nonarboreal) and predominantly herbivorous muroids in the tropical grassland ecosystems they inhabit. Apparently, other ecologically similar New World muroid taxa occupy temperate latitudes.

Since the genus *Sigmodon* is restricted to open habitats, the distribution and relationships of cotton rat species presumably reflect the Late Cenozoic history of forested and unforested landscapes in North and South America. Some historical-biogeographic implications of the distributional data reported here are considered briefly, but phylogenetic information is required to discriminate among alternative scenarios. The sampling design of cladistic studies to obtain such information is discussed.

RESUMEN

Los roedores muroides del género *Sigmodon* alcanzan desde Iowa y Nebraska (en los Estados Unidos) hasta Perú y Surinam. Siete especies válidas se reconocen actualmente en América del Norte y América Central, pero las doce especies nominales conocidas de América del Sur no han recibido atención taxonómica crítica hasta la fecha. Esta revisión, basada en los caracteres morfológicos de casi 1300 especímenes, demuestra que existen cuatro especies diagnosticables en la fauna de América del Sur. Los especímenes sin surcos en los incisivos superiores, de Colombia y del noroeste de Venezuela, se asemejan mucho al típico *hispidus* en todas las comparaciones cualitativas y

cuantitativas (incluyendo cariotipos), y se refieren provisionalmente a la misma especie. Especímenes de *alstoni*, una rata más pequeña con surcos profundos en los incisivos superiores, proporciones craniodentales distintivas, y cariotipos muy divergentes, han sido encontrados simpátricamente con *hispidus* en varias localidades; esta especie alcanza desde el extremo noreste de Colombia, por todas partes de Venezuela, hasta unas localidades dispersas en Guyana, Surinam, y Brasil al norte del río Amazonas. Una tercera especie, *peruanus*, está restringida al litoral Pacífico y las estribaciones Andinas adyacentes del Ecuador y el noroeste de Perú; se puede distinguir *peruanus* de

hispidus y de las otras especies congénicas por muchos caracteres cualitativos y cuantitativos craneodentales, incluyendo un patrón único de la circulación estapedial. Conocido solamente de dos localidades en los altos Andes del Ecuador, *inopinatus* es muy divergente de las otras especies en la morfología del rostro y de la región interorbital.

La información disponible sobre la historia natural sugiere que las especies suramericanas de *Sigmodon*, como las de América del Norte, se encuentran en los habitats abiertos (no boscosos), son activos de día y de noche, construyen pistas o caminos, y consumen principalmente los tejidos verdes de gramíneas y otras hierbas. Las comparaciones con dos taxa simpátricos, *Zygodontomys* y *Holochilus*, sugieren que las especies de *Sigmodon* son los únicos roedores muróides estrictamente terrestres (no acuáticos y no boscosos) y

principalmente herbívoros en las sabanas tropicales que ellos habitan. Aparentemente, otros muróides del Nuevo Mundo semejantes a *Sigmodon* en estos aspectos ecológicos se encuentran en latitudes templadas.

Como el género *Sigmodon* se encuentra solamente en los habitats abiertos, la distribución y las relaciones filogenéticas de las especies del mismo por presunción reflejan la historia cuaternaria de los bosques y las sabanas en América del Norte y del Sur. Algunos significados históricos y biogeográficos de los datos distribucionales proporcionados aquí se consideran brevemente, pero son necesarias reconstrucciones filogenéticas para probar los escenarios alternativos. El diseño de muestreo para comparaciones morfológicas, citogenéticas, o moleculares para obtener dichas reconstrucciones también se discute.

INTRODUCTION

Species of the muroid rodent genus *Sigmodon*, commonly known as cotton rats, are abundant in much of the continental United States, especially in the prairies of the southernmost plains states, in southwestern desert grasslands and mountain meadows, in the open pine forests and fallow agricultural fields of the southeast, and generally wherever grass is a significant component of the local vegetation. Further south, species of *Sigmodon* also occur in tropical lowland savannas and in the high-altitude Andean grasslands known as *páramos*. Since Say and Ord's (1825) discovery of the type species, *S. hispidus*, a total of 69 nominal taxa of Recent *Sigmodon* have been described. Modern concepts of species limits and relationships among North American representatives of the genus (summarized by Hall, 1981) are largely the outgrowth of seminal papers by Baker (1969) and Zimmerman (1970) that provoked numerous cytological studies of populations in the United States and Mexico. Hoffmeister's (1986) synthesis of morphological, karyological, and ecological information for the Arizona species is an exemplary result of careful systematic research in an exceptionally well-collected region, but elsewhere systematic treatments of *Sigmodon* have usually been perfunctory. For the South American taxa, there is no revisionary literature at all.

The nomenclatural history of Neotropical cotton rats was reviewed by Tate (1932), who listed 12 nominal species from South Amer-

ica: 9 with ungrooved upper incisors were referred to *Sigmodon*, and 3 with grooved teeth were classified as *Sigmomys* following Thomas (1901, 1914). Hershkovitz (1955) thought that all cotton rats (whether smooth-toothed or groove-toothed) might be conspecific, but Cabrera (1961) only synonymized *Sigmomys* with *Sigmodon* while retaining *hispidus* (including all the smooth-toothed South American forms) and *alstoni* (including all the groove-toothed taxa) as valid species. Although both Handley (1972) and Reig (1986) recognized four South American species of *Sigmodon* (including *Sigmomys*), most checklists (e.g., Corbet and Hill, 1980; Honacki et al., 1982) have followed Cabrera (1961). Unfortunately, none of these diverse classifications are accompanied by analyses or substantive discussions of character data, and it is therefore impossible to evaluate the empirical basis for any taxonomic alternative without extensive recourse to specimens.

This report provides the first critical revision of South American *Sigmodon*, summarizes anatomical character variation within and among species, maps geographic ranges, and includes such natural history information as can be gleaned from fieldnotes and the scant published literature. Taken together, these data reveal endemic ecomorphological distributions that must be accommodated in historical reconstructions of cotton rat biogeography. Alternative biogeographic scenarios are briefly considered, and

efforts to obtain the phylogenetic information required to test them are encouraged.

ACKNOWLEDGMENTS

The research described herein is based on data obtained from museum specimens. Those specimens, together with the labels and fieldnotes that accompany them, represent the efforts of numerous individuals and institutions committed to a worldwide inventory of biological diversity. Because the personal and financial commitments that make such collection resources available for research are increasingly challenged by the demands of other societal priorities, I gratefully acknowledge the important contributions of the following institutions and their professional staffs: the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); the Field Museum of Natural History, Chicago (FMNH); the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); the Museo de Historia Natural La Salle, Caracas (MHNLS); the Museum National d'Histoire Naturelle, Paris (MNHN); the Museum of Vertebrate Zoology, Berkeley (MVZ); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); the Royal Ontario Museum, Toronto (ROM); the Texas Cooperative Wildlife Collection, College Station (TCWC); the University of Michigan Museum of Zoology, Ann Arbor (UMMZ); and the National Museum of Natural History, Washington D.C. (USNM).

Victoria L. Mayer, a former Research Assistant in the Department of Mammalogy, provided much valuable assistance at an early stage of this research: she reorganized and recurated our *Sigmodon* collections, compiled locality information for the gazetteer from fieldnotes in our archives, and spent long hours in the library tracking down obscure references for the bibliography. Without her help this report would have been substantially longer in preparation.

It is a pleasure to thank the Museo de Historia Natural La Salle and its director, Giuseppe Colonnello, for logistical support while I was in Venezuela in 1986 and 1987. My fieldwork there would have been much less productive and enjoyable without the enthusiastic assistance of Helen Kafka, Hernán

Castellanos, Isa Torrealba, Carlos Gauveca, Carlos Lasso, and Pablo Morales. Collecting and export permits were kindly provided by the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables.

The splendid line drawings and cranial photographs that illustrate this report reflect the artistic talents of Patricia Wynne and Peter Goldberg, respectively. Bill Barnett and Peiling Fong are responsible for the SEM images of teeth, and Erika Bach provided preliminary analyses of karyotypes.

Phil Myers, Bruce Patterson, and Nancy Simmons read the manuscript and provided helpful criticisms; their generous contribution of time and effort to improve this report is sincerely appreciated.

MATERIALS AND METHODS

SPECIMENS

The 1273 specimens examined in the course of this research are deposited in the museum collections listed with their standard abbreviations in the Acknowledgments, above. Information provided in the species accounts that follow, under the heading Specimens Examined, consists of the number of specimens from which data were recorded (listed by museum collection) for each locality. Catalog numbers are provided in the Appendix for specimens whose measurements are summarized by statistics tabulated in the text.

MEASUREMENTS

Total length (TL), length of tail (LT), and length of the hindfoot (HF) were recorded from specimen labels, but I remeasured dried hindfeet (including the claws) whenever possible; length of head-and-body (HBL) was calculated by subtracting LT from TL. Tabulated means of external measurements are from specimens collected by field workers who are known or presumed to have followed the American measurement conventions described by Hall (1981).

The following craniodental measurements were determined with dial calipers as described and illustrated by Voss (1991): condylo-incisive length (CIL); length of diastema (LD); occlusal length of molars (LM); breadth of M1 (BM1); length of incisive foramen

(LIF); breadth of rostrum (BR); breadth of palatal bridge (BPB); breadth of zygomatic plate (BZP); least interorbital breadth (LIB); and depth of incisor (DI). Breadth of the incisor tips (BIT) was measured across the enameled bands of both upper teeth, and zygomatic breadth (ZB) across the squamosal zygomatic roots, as illustrated by Voss (1988).

AGE CRITERIA

Species of *Sigmodon* do not exhibit the marked ontogenetic transformations of post-natal morphology that permit operational definitions of age categories in other muroids: the pelage of even the smallest juveniles closely resembles that of large adults, and molar occlusal morphology is not much affected by wear. Unfortunately, the criteria for age determination in *S. hispidus* proposed by Chipman (1965) cannot be determined by convenient, nondestructive methods from standard museum preparations. I reserve the term "juvenile" for animals with incompletely erupted or unworn third molars, and "old adult" for specimens with molars worn below the widest part of the crowns. All other specimens, regardless of apparent age differences among them, are considered "adult" in the present report.

KARYOTYPES

Karyotypic information newly reported here was obtained from metaphase preparations of bone marrow cells. Specimens were processed in the field, initially by subcutaneous injections of live yeast cultures, followed after 12 to 24 hours by minor modifications of standard *in vivo* colchicine/hypotonic citrate methods (Patton, 1967). Cell suspensions were fixed in Carnoy's solution and frozen in liquid nitrogen for transport to the laboratory where they were flame-dried on glass slides and stained with Giemsa. Only modal diploid counts are provided from our incomplete analyses.

MULTIVARIATE STATISTICS

All multivariate statistics reported herein were computed from measurement values transformed to their natural logarithms. Cluster analyses based on Mahalanobis distances, and principal components analyses,

were executed under the assumptions and following the procedures explained by Voss (1991). General-size coefficients were estimated as the elements of the first eigenvector of the pooled within-group covariance matrix; the normalized coefficients of general-size-invariant group differences were computed as described by Voss and Marcus (in press). The interpretation of general-size coefficients in terms of ontogenetic allometry, and the growth-invariance of the residual within- and between-sample variation is discussed extensively by Voss et al. (1990) and by Voss and Marcus (in press).

GAZETTEER

South American localities from which *Sigmodon* species have been collected are listed alphabetically below. Numbering is sequential only within countries; italic type identifies subordinate political units (departments, states, provinces, etc.), and boldface identifies locality names as cited in the text of this report. Latitude (degrees and minutes N or S) and longitude (degrees and minutes W) are given in parentheses without punctuation (e.g., 0230N/5600 for 2°30'N, 56°00'W). Most of the geographical coordinates provided herein agree with those listed in gazetteers published by the Office of Geography, U.S. Department of the Interior (cited as USBGN by Paynter and his colleagues, e.g., Paynter and Traylor, 1991), but I have not hesitated to use other sources that appeared more authoritative for some areas (e.g., Handley, 1976). Elevations are reported verbatim (in feet or meters) from specimen labels, field-notes, or cited secondary sources. Localities are mapped in figures 1 and 2.

BRAZIL

1. **Pará**, **Serra do Tumucumaque**, 12 km da Guiana Holandeza (ca. 0230N/5600).
2. **Roraima**, **Frechal** (= Frexal; 0350N/6032).
3. **Roraima**, Rio Cotinga, **Limo** (0356N/6030); elevation ca. 1500 ft (Tate, 1939).
4. **Roraima**, **Serra da Lua** (0215N/6045); elevation ca. 300 m (Paynter and Traylor, 1991). This locality is presumed synonymous with the "Moon Mountains" of early collectors who thought they were in British Guiana (Guyana).

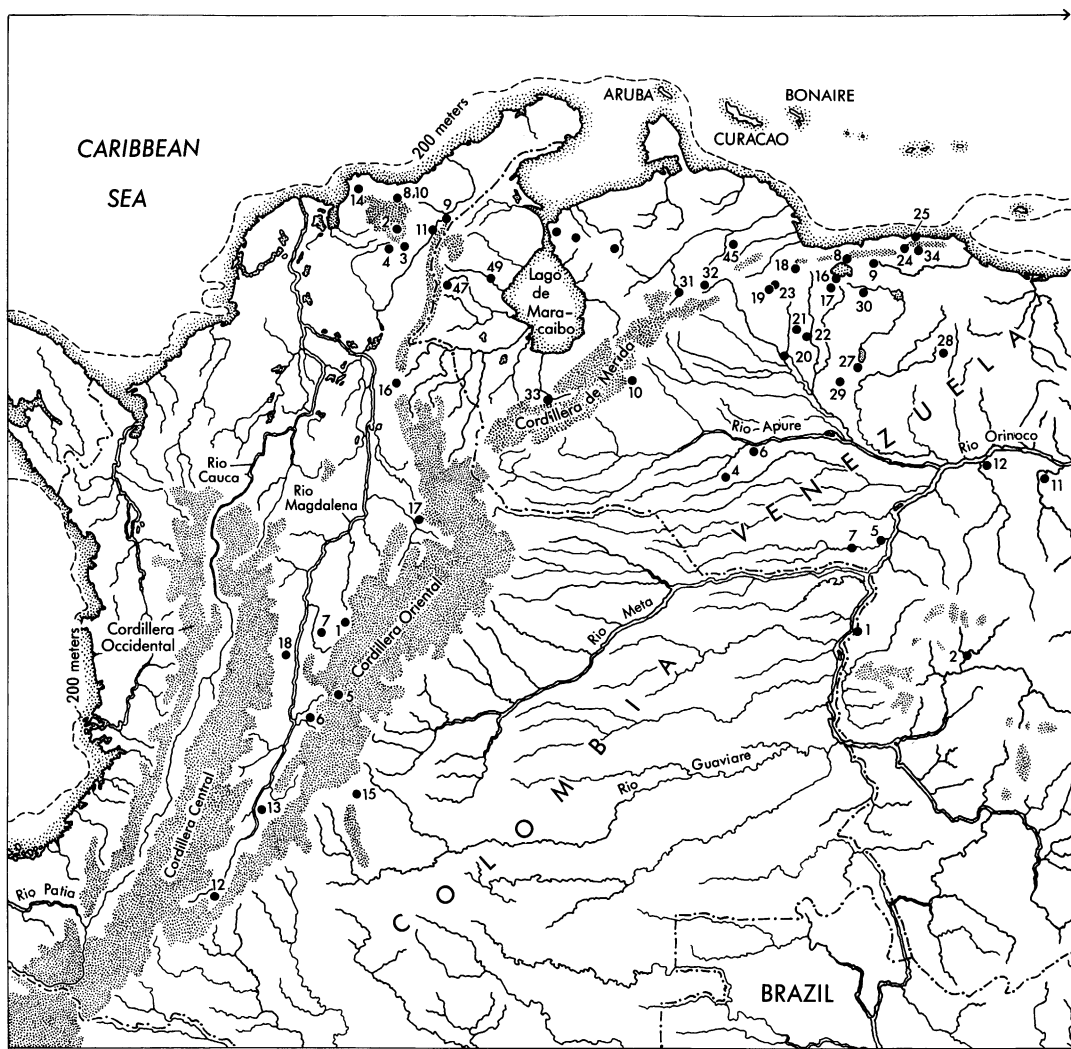
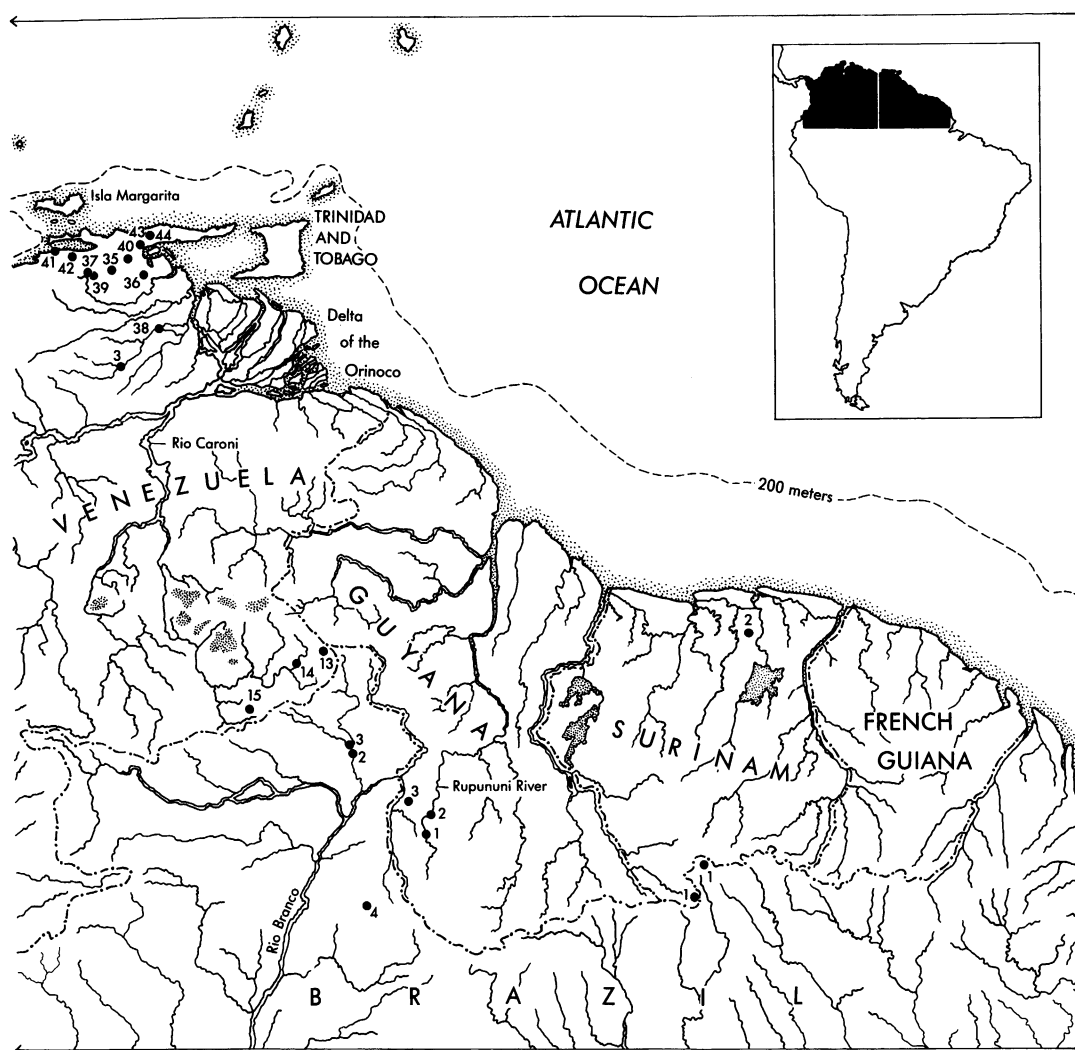


Fig. 1. Collection localities in Colombia, Venezuela, the Guianas, and Brazil. Densely stippled land areas are those above 1500 m elevation.

COLOMBIA

1. *Boyacá*, **Muzo** (0532N/7406); elevation 1240 m (Paynter and Traylor, 1981).
2. *Cesar*, **El Mamón** (1037N/7333), **Pueblo Viejo** (?1032N/7325), and **San Sebastian** (1034N/7336) in the Sierra Nevada de Santa Marta; elevations recorded on W. W. Brown's specimen tags are 8000–9000 ft at El Mamón, 8000 ft at Pueblo Viejo, and 6600 ft at San Sebastian.
3. *Cesar*, **El Salado** (1022N/7329), NW of Valledupar (1029N/7315); elevation 430 m (Hershkovitz, 1960).
4. *Cesar*, **Pueblo Bello** (1024N/7343); elevation 1067 m (Hershkovitz, 1960).
5. *Cundinamarca*, **Bogotá** (0436N/7405), including "Plains of Bogota" and "Quebrada Seca"; elevation 2590 m (Paynter and Traylor, 1981).
6. *Cundinamarca*, **10 km E Boquerón** (0416N/7433); elevation (at Boquerón) ca. 400 m (Paynter and Traylor, 1981).
7. *Cundinamarca*, **Caparrapi** (0521N/7430), Los Volcanes; elevation ca. 1250 m (from map).
8. *Guajira*, **La Concepción** (ca. 1103N/



- 7327); elevation ca. 800 m (Paynter and Traylor, 1981).
9. **Guajira, Las Marimondas** (1052N/7243), in the Sierra de Perijá; elevation 1000 m (Hershkovitz, 1960).
 10. **Guajira, San Antonio** (1103N/7326); elevation 3450 ft (Paynter and Traylor, 1981).
 11. **Guajira, Sierra Negra** (1036N/7255), in the Sierra de Perijá E of Villanueva, and **Villanueva** (1037N/7259); elevation 274 m at Villanueva and 1265 m at Sierra Negra (Hershkovitz, 1960).
 12. **Huila, Valle de Suaza** (mouth of Río Suaza is at 0210N/7541, but most sub-localities probably to SW; the only one listed by USBGN is Marmato at 0155N/7642), including C. del Aguila's sublocalities Avispero, Belgica, Guapaton, Mantagua, Marmato, Naranjal, Picuma, San Calixto, and San Isidro.
 13. **Huila, 17 km SE Villavieja** (0313N/7514); elevation 1600 ft.
 14. **Magdalena, Agua Dulce** (ca. 1106N/7407), **Bonda** (1114N/7408), **Cincinnati** (1106N/7406), **Mamatoco** (= Mamato-

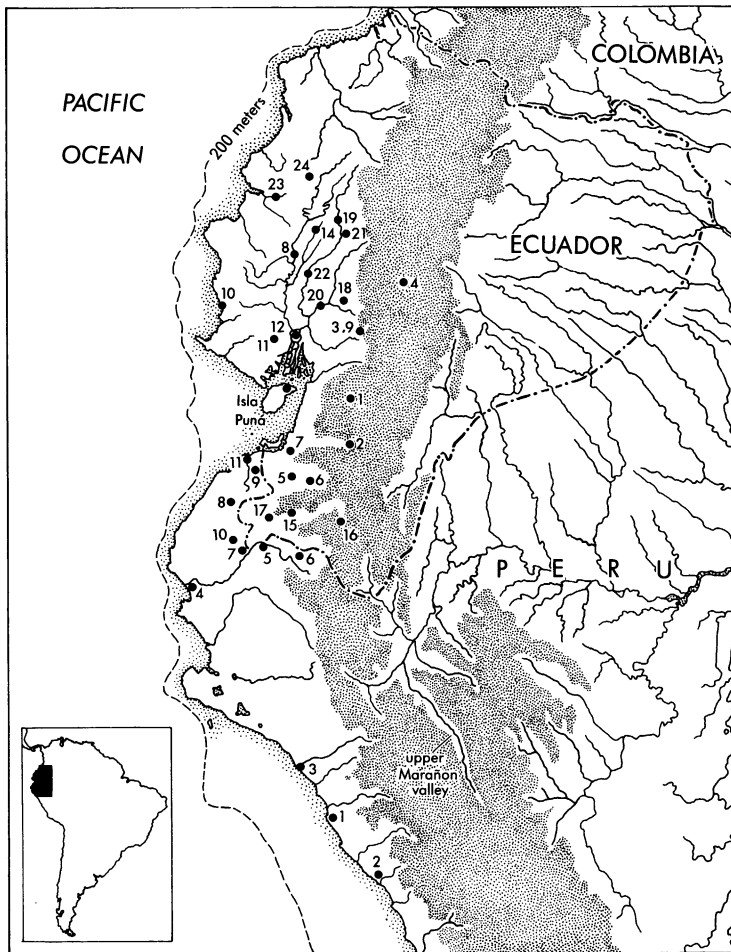


Fig. 2. Collection localities in Ecuador and Peru. Densely stippled land areas are those above 1500 m elevation.

ca, 1114N/7410), **Manzanares** (1114N/7413; but possibly a community and not the river), **Masinga** and **Masinga Vieja** (both at ca. 1116N/7405), **Minca** (1109N/7407), **Onaca** (1111N/7404), and “**Santa Marta**” (no coordinates; probably a general reference to the whole sierra and not the coastal town); from near sea level on the Caribbean coastal plain to about 3500 ft in the adjoining northwestern foothills of the Sierra Nevada de Santa Marta.

15. **Meta**, San Juan de Arama, **Los Micos** (0317N/7353); elevation 450 m (Paynter and Traylor, 1981).
16. **Norte de Santander**, **Guamalito** (0834N/

7329); elevation ca. 400 m (Paynter and Traylor, 1981).

17. **Santander**, **Bucaramanga** (0708N/7309); elevations from 1050 to 1100 m.
18. **Tolima**, **Mariquita** (0512N/7454); elevation 3000 ft.

ECUADOR

1. **Azuay**, **Las Cajas National Park** (0253S/7919), including “Torreadora” and “Lake Luspá”; elevations on A. Barnett’s specimen tags are 3750 and 3800 m.
2. **Azuay**, **Tunguilla Valley** (= Valle de Yunguilla; 0318S/7918); elevation 1500 m.

3. *Chimborazo, Puente de Chimbo* (0210S/7910) near Bucay (0210S/7906); elevation 1200 ft.
4. *Chimborazo, Urbina* (0130S/7844); elevation 11,400 ft (Anthony, 1924).
5. *El Oro, Piedras* (0338S/7955); elevation 300 m.
6. *El Oro, Portovelo* (0343S/7939); elevation 2000 ft.
7. *El Oro, Santa Rosa* (0327S/7958); elevation 100 ft.
8. *Guayas, Balzar Mountains* (= Balzar, 0122S/7954); elevation 100 m (a misnomer, see Paynter and Traylor, 1977).
9. *Guayas, Bucay* (0210S/7906); elevations from 900 to 1000 ft.
10. *Guayas, Cerro Manglaralto* (presumably near Manglaralto at 0150S/8044) and *Hacienda El Refugio* (5 km E Manglaralto); elevation 1200 ft at Cerro Manglaralto, but Manglaralto is at sea level according to Paynter and Traylor, 1977).
11. *Guayas, Chongón* (0214S/8004) and *Chongoncito* (east of Chongon); elevation 60 m at Chongón, but Chongoncito is at sea level according to G. H. H. Tate's fieldnotes (AMNH Department of Mammalogy archives).
12. *Guayas, Guayaquil* (0210S/7950), *Durán* (= Alfaro; 0212S/7950), and *G and Q RR kilometer 8*; near sea level.
13. *Guayas, Puná and San Ramón*, both on Isla Puná (0250S/8008); near sea level.
14. *Guayas, Pacaritambo*, Cantón de Balzar, 30 km S Quevedo (0102S/7929).
15. *Loja, Casanga Valley* near Guachanamá (0402S/7953) and Celica (0407S/7959); elevation 2900 ft.
16. *Loja, Malacatos* (0414S/7915); elevation 1600 m.
17. *Loja, Pindal* (0409S/8010).
18. *Los Ríos(?), Limón*, on road from Balzapamba (= Balzapamba; 0147S/7913) to Babahoyo (0149S/7931); elevation 1200 ft.
19. *Los Ríos, Quevedo* (0102S/7929); elevation ca. 100 m (Paynter and Traylor, 1977).
20. *Los Ríos, Río Babahoyo* near Pimocha (0152S/7935), including "Río Babahoyo," "Río Babahoyo-Pimocha," and "Río Babahoyo/Pimocha-Sur."
21. *Los Ríos, 1.5 km S San Carlos*, on road

from Quevedo (0102S/7929) to Babahoyo (0149S/7931).

22. *Los Ríos, Vices* (0132S/7945), including nearby settlements Hacienda Pijigual and Hacienda Santa Teresa (ca. 12 km NE Vices); elevation 100 ft at Hacienda Pijigual.
23. *Manabí, Chone* (0041S/8006); elevation 20 m (Paynter and Traylor, 1977).
24. *Manabí, Río de Oro* (ca. 0028S/7936).

GUYANA

1. *Rupununi, Dadanawa* (0250N/5930), including Dadanawa Ranch and 15 mi ENE Dadanawa; elevation ca. 150 m (Stephens and Traylor, 1985).
2. *Rupununi, Kanuku Mountains* (ca. 0312N/5930), including J. J. Quelch's localities Kwaimattat (?= Kwaimatta), Pirasa, Rupununi River, and Upocarit; elevation 240 ft.
3. *Rupununi, Nappi Creek* near Lethem (0323N/5948); elevation 107 m at Lethem (Stephens and Traylor, 1985).

PERU

1. *La Libertad, Pacasmayo* (0724S/7934); elevation 8 m (Stephens and Traylor, 1983).
2. *La Libertad, Trujillo* (0807S/7902); elevation 200 ft.
3. *Lambayeque, Eten* (0654S/7952); elevation 10–15 m.
4. *Piura, Hacienda Laredo, El Arenal* (0455S/8102).
5. *Piura, Huásimo* (0419S/8012); elevation 750 m.
6. *Piura, Jilili* (0435S/7949); elevation between 1000 and 2000 m (from map).
7. *Piura, Lancones* (0435S/8028).
8. *Tumbes, El Sauce* (0403S/8034).
9. *Tumbes, Matapalo* (0341S/8012); elevation 54 m (Stephens and Traylor, 1983).
10. *Tumbes, Positos* (0417S/8031); elevation 25 m.
11. *Tumbes, Tumbes* (0334S/8028); sea level.

SURINAM

1. *Nickerie, Sipaliwini-savanne-vliegeveld* (0205N/5610); elevation ca. 358 m (Stephens and Traylor, 1985).

2. *Para*, **Zanderij** (0527N/5512); elevation ca. 50 m (Stephens and Traylor, 1985).

VENEZUELA

1. *Amazonas*, **Paria Grande** (25 km SSE Puerto Ayacucho [0540N/6735]) and **Rueda** (18 km SSE Puerto Ayacucho); elevation 119 m at Paria Grande and 125 m at Rueda.
2. *Amazonas*, **San Juan Manapiare** (0518N/6613); elevation 155 m (Hendley, 1976).
3. *Anzoátegui*, **Río Oritupano** (ca. 0857N/6322); elevation 200 m.
4. *Apure*, **Entrada La Yaguaita**, Mantecal (0733N/6909); elevation 12 m (ca. 75 m according to Paynter, 1982).
5. *Apure*, **Hato Cariben** (0633N/6713), 60 km NE Puerto Páez; elevation 76 m.
6. *Apure*, **Hato El Frio**, 31 km (by road) W El Samán de Apure (0755N/6844); elevation 60 m.
7. *Apure*, **41 km NW Puerto Páez** (0613N/6728 at Puerto Páez); elevation 76 m.
8. *Aragua*, **Rancho Grande** (1022N/6741), including El Limón (1018N/6738), and Guamita; Rancho Grande is situated at ca. 900–1000 m just below the crest of the coastal cordillera in the Lago Valencia catchment, while Guamita (at 700 m) and El Limón (524 m) are in the foothills a few km NW of Maracay (1015N/6736).
9. *Aragua*, **Tiara** (ca. 1011N/6709), including adjacent localities in the Cordillera del Interior ESE of Maracay (1015N/6736), including Agua Amarilla, El Limoncito, La Esperanza, and La Horqueta; and **Camp Rangel** (= Camp Rafael Rangel and Campamento Rangel).
10. *Barinas*, near **Altamira** (0850N/7030); elevations from 600 to 1070 m (Hendley, 1976).
11. *Bolívar*, **El Llagual** (= El Yagual at ca. 0725N/6510); elevation ca. 100 m (Paynter, 1982).
12. *Bolívar*, **Hato La Florida** (ca. 0727N/6546); elevations from 43 to 68 m.
13. *Bolívar*, **Mount Roraima**, including Arabopó (also spelled "Arabupu"; 0506N/6044) and Paulo (0508N/6049); elevation 4200 ft at Arabopó and 4000 ft at Paulo. These localities were correctly mapped by Tate (1930) in Venezuela, but his specimen tags say Brazil.
14. *Bolívar*, **San Ignacio Yuruaní** (ca. 0502N/6108); elevation 850 m.
15. *Bolívar*, **Vetania**, 46 km N Icabarú (0420N/6146); elevation 800 m (Hendley, 1976).
16. *Carabobo*, **El Trompillo** (1004N/6746), near Lago Valencia; elevation 1300 ft (Thomas, 1914).
17. *Carabobo*, **La Florida** (?0956N/6747), Serranía de Barbula; elevation 1050 m.
18. *Carabobo*, near **Montalbán** (1013N/6820); elevations from 1055 to 1091 m.
19. *Cojedes*, "El Candelo," **Tucuragua** (0954N/6841), SW La Sierra; elevation 640 m.
20. *Cojedes*, **Hato El Tirado** (?0910N/6823).
21. *Cojedes*, **Hato Itabana**, 38 km SE Las Vegas (0935N/6837); elevation 80 m.
22. *Cojedes*, **Hato Los Caballos**, on the road from Tinaco (0942N/6826) to El Baúl (0857N/6817); elevation 210 m.
23. *Cojedes*, **La Blanquera** (ca. 0957N/6836), Cerro Azul; elevation 1100 m (Paynter, 1982).
24. *Distrito Federal*, **Caracas** (1030N/6655), including Los Venados (5 km N Caracas) and "Phelps Hill"; elevation 950 m at Phelps Hill and 1485–1580 m at Los Venados.
25. *Distrito Federal*, **San Julián** (ca. 1037N/6650); sea level (Paynter, 1982).
26. *Falcón*, **Cerro Socopo** (1028N/7048); elevation 1260–1265 m.
27. *Guárico*, **Calabozo** (0856N/6726), Alberto Ablan Farm; elevation ca. 100 m at Calabozo (Paynter, 1982).
28. *Guárico*, **Hato La Merrereña**, Las Mercedes (0907N/6624); elevation ca. 220 m at Las Mercedes (Paynter, 1982).
29. *Guárico*, **Parcela 200**, ca. 20 km SW Calabozo (0856N/6726); elevation less than 500 m (from map).
30. *Guárico*, **San Juan de los Morros** (0955N/6721).
31. *Lara*, **Caserio Boro**, 10 km N El Tocuyo (0947N/6948); elevations from 518 to 537 m.
32. *Lara*, vicinity of **San Miguel** (0953N/6931), including localities "Camp No. 1," "La Fortuna," "Palenque," "San Gerónimo," "San Rafael," and "east side of Turbia valley" sampled by the Scarritt Venezuelan Expedition in 1938; elevations from 960 to 2500 m.

33. *Mérida*, near **Mesa Bolívar** (0826N/7134); elevation 690 m (Handley, 1976).
34. *Miranda*, **Curupao** (1031N/6638), 19 km E Caracas; elevation 1160 m.
35. *Monagas*, near **Caripe** (1012N/6329); elevation 1180 m.
36. *Monagas*, **Caripito** (1008N/6306); elevation ca. 100 m (Paynter, 1982).
37. *Monagas*, **Cocollar** (1010N/6347), including Río Cocoyal; elevations from 1575 to 2600 ft.
38. *Monagas*, **Hato Mata de Bejuco**, 47–54 km SE Maturín (0945N/6311 at Maturín); elevations from 18 to 36 m.
39. *Monagas* and *Sucre*, **San Antonio Maturín** (1007N/6343) and **Campo Alegre** (ca. 1010N/6345); elevations from 1500 to 1800 ft at San Antonio.
- . *Portuguesa*, **Los Mamones**, Finca Santa Rita (not located).
40. *Sucre*, **40 km NW Caripito** (1008N/6306 at Caripito).
41. *Sucre*, near **Cumaná** (1028N/6410); sea level.
42. *Sucre*, **Cumanacoa** (1015N/6355); elevation 700 ft.
43. *Sucre*, **Finca Vuelta Larga**, 9.7 km (by road) SE Guaraúnos (1033N/6307); elevation 10 m.
44. *Sucre*, **Manacal** (1037N/6301), 25 km E Carúpano (1040N/6314); elevations from 411 to 424 m.
45. *Yaracuy*, **Finca El Jaguar**, ca. 20 km NW Aroa (1026N/6854); elevation 690 m.
46. *Zulia*, **Empalado Savannas**, ca. 30 mi E El Panorama (ca. 1040N/7125); near sea level (Paynter, 1982).
47. *Zulia*, **Novito** (1002N/7243), 19 km WSW Machiques; elevation 1135 m.
48. *Zulia*, **Río Aurare** (= Río Anaure), probably near El Panorama (ca. 1040N/7125); near sea level (from map).
49. *Zulia*, **Río Cogollo** (?1015N/7230); elevation 350 ft (Paynter, 1982).

THE GENUS

Descriptions of *Sigmodon* provided by Say and Ord (1825), Coues (1877), Gyldenstolpe (1932), and Ellerman (1941) are inadequate for the purposes of this report: the genus now includes *Sigmomys* as a subjective junior synonym, many new characters have been discovered by muroid morphologists in recent decades, and close study of the South

American species has revealed an unexpected range of variation even in traditional character complexes. This section summarizes taxonomic, morphological, and geographical information about the genus as a whole, and evaluates prior conjectures concerning its phylogenetic relationships.

Sigmodon Say and Ord

Sigmodon Say and Ord, 1825: 354.

Lasiomys Burmeister, 1854: 16.

Deilemys Saussure, 1860: 98.

Sigmomys Thomas, 1901: 150.

TYPE SPECIES: *Sigmodon hispidus* Say and Ord (1825), based on three specimens collected in 1818 “in East Florida,” probably from abandoned plantations along the St. Johns River where the animal was found to be abundant (op. cit.: 355). The type series, originally deposited in the Philadelphia Museum, is not extant² but Say and Ord’s illustration (fig. 3) and description are sufficient to establish the name as pertaining to only one currently recognized muroid species in Florida. Bailey (1902) and Hall (1981) gave the type locality of *S. h. hispidus* as “St. Johns River, Florida,” but Hall illogically included the entire course of that river in the mapped range of *S. h. floridanus* (op. cit.: 738). For comparisons with the South American taxa treated in this paper, a very large series of specimens from the vicinity of Lake Placid in Highlands County, Florida is assumed to represent the typical morphology of *hispidus* (figs. 4, 5).

DISTRIBUTION: From about 41°N (in Iowa and Nebraska) throughout most of the southern, southeastern, and southwestern United States, Mexico, and Central America (see

² The natural history collections of the Philadelphia Museum (also known as the Peale Museum) were sold in 1850 to P. T. Barnum and Moses Kimball. Barnum’s half of the collections was destroyed by fire in New York in 1865, but Kimball’s was deposited in the Boston Museum and later (in 1893 and 1899) given to the Boston Society of Natural History. Some of the latter material was destroyed by the Society, and the original labels of the remaining specimens were removed and lost. The surviving, unlabeled remnants of the Peale Museum were finally obtained by the Museum of Comparative Zoology at Harvard University in 1914, but the type series of *Sigmodon hispidus* was apparently not among them (Allen, 1931). The sad history of the Peale Museum’s important collections is chronicled by Barbour (1946).

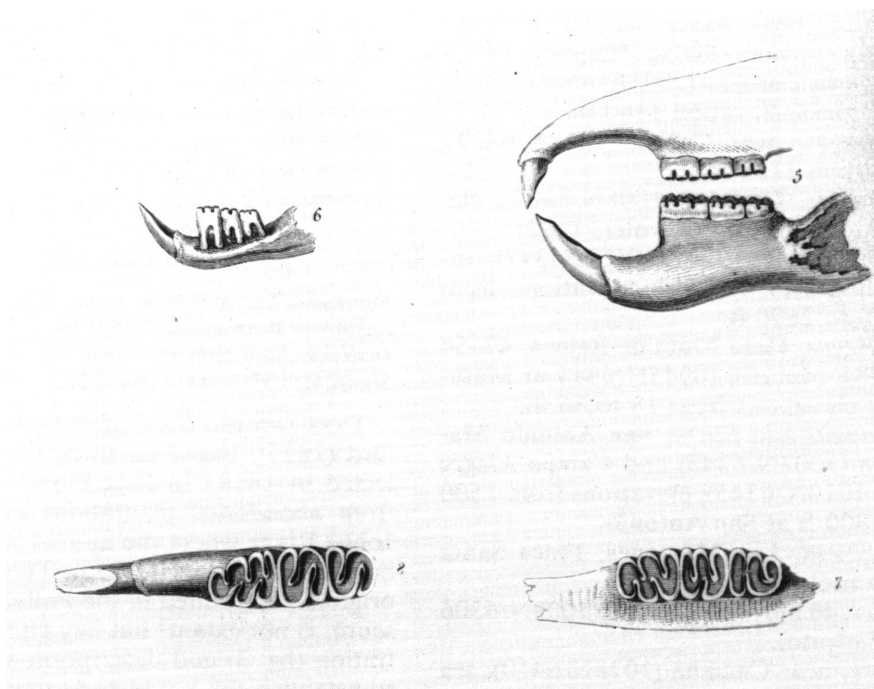


Fig. 3. Say and Ord's (1825) illustration of *Sigmodon hispidus*.

Hall, 1981: maps 426–431), to northern South America. In South America, the genus occurs from Colombia southward to northwestern Peru, and eastward at least as far as Surinam.

DIAGNOSIS: Small-eared, short-whiskered, and short-tailed rodents of the muroid subfamily Sigmodontinae (sensu Carleton and Musser, 1984) with coarsely grizzled, brownish dorsal pelage; hindfoot unwebbed, with three middle digits (II, III, and IV) much longer than outer digits (I and V); mammae ten (in five pairs) or eight (in four pairs); convergent, beaded postorbital margins of skull continuous with prominent temporal crests; zygomatic notches deeply excavated; inferior zygomatic root broad, with spinous anterodorsal process; parapterygoid fossae deeply excavated; alisphenoid strut present (buccinator-masticatory foramen and foramen ovale accessorius separate); tegmen tympani overlaps posterior margin of squamosal anterodorsal to bulla; molars hypsodont and conspicuously lophodont, with principal cusps and crests deployed in sigmoidal arrays; anterocone(id) of M1/m1 undivided; mesoloph(id)s absent; first upper molar with four roots; first lower molar with three or four

roots; stomach unilocular and hemiglandular; gall bladder present; preputial glands in two pairs; glans penis complex, with tridigitate baculum.

DESCRIPTION: Pelage coarse, short, and close in lowland forms, but deeper and softer in populations from higher elevations; always coarsely grizzled-brownish dorsally, but ventral pigmentation variable within and among species; ears small but always visible, sparsely haired in lowland forms but furry in populations and species from high elevations. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present; mystacial vibrissae short, never extending beyond pinnae when laid flat against cheek. Manus and pes well-haired dorsally, but without conspicuous tufts of longer hairs at bases of claws; entirely naked on plantar surfaces (including heel of pes); manus with five plantar tubercles (two carpal and three interdigital pads); pes with six plantar tubercles (two metatarsal and four interdigital pads); digits I and V of pes always much shorter than adjacent digits II and IV (claw of I never extending to first interphalangeal joint of II, claw of V extending to but not beyond first

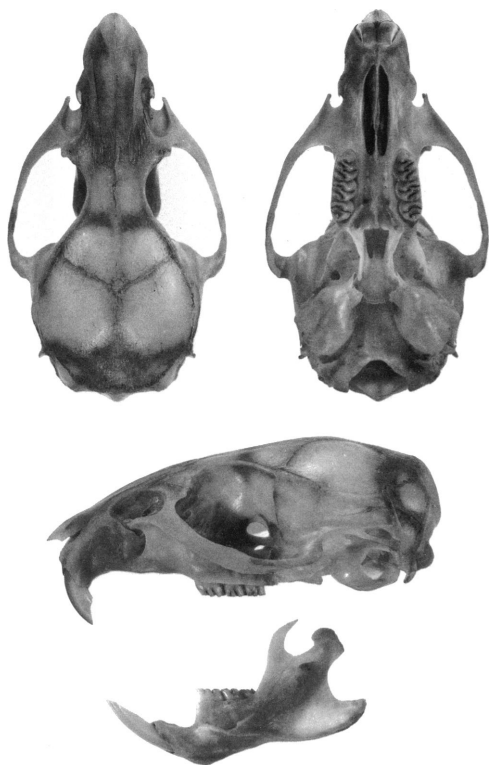


Fig. 4. Cranium and mandible of *Sigmodon hispidus* (AMNH 255414) from 8 mi S Lake Placid, Highlands County, Florida.

interphalangeal joint of IV).³ Tail indistinctly or sharply bicolored (dark above and paler below); always shorter than combined length of head-and-body; sparsely haired in lowland species (tails of highland forms are more densely haired but epidermal scales are never completely concealed); tail tip without conspicuous tuft or pencil of longer hairs. Mam-mae usually ten in inguinal, abdominal, thoracic, postaxial, and pectoral pairs (but some specimens of *hispidus* have eight or twelve teats [Meyer and Meyer, 1944] and thoracic teats are apparently absent in most specimens of *inopinatus*).

Skull distinctive in dorsal view, with stout rostrum flanked by deeply excavated zygomatic notches; nasals long (concealing incisors from dorsal view) or short (incisors visible dorsally); posterior supraorbital margins

³ Hall's (1981: 736) illustration of *S. hispidus* erroneously shows the hindfoot with a very long fifth digit.

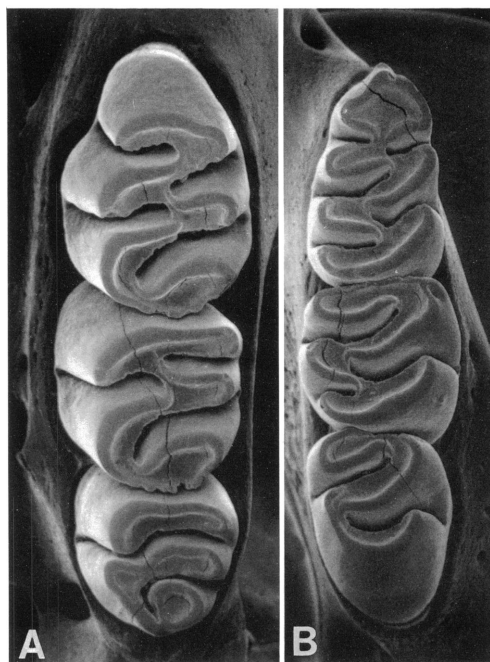


Fig. 5. Left maxillary (A) and right mandibular (B) molar series of *Sigmodon hispidus* (AMNH 255409) from 8 mi S Lake Placid, Highlands County, Florida.

convergent and beaded; supraorbital beads continuous with prominent temporal crests along dorsolateral contours of braincase; zygomatic arches usually convergent (widest across the squamosal roots); interparietal usually large (but reduced and sometimes absent in *leucotis*). Rostrum short and deep in lateral view; zygomatic plate broad, with concave anterior margin and spinous anterodorsal process. Incisive foramina long (extending posteriorly to or between the molar alveoli) or short (not so extending). Morphology of palatal bridge highly variable among species; long or short, broad or narrow (sensu Hershkovitz, 1962); with or without median keel, posterolateral sulci, and median posterior spinous process. Anterior limit of mesopterygoid fossa correspondingly diverse in position and configuration, but roof of mesopterygoid fossa always fenestrated by large sphenopalatine vacuities. Parapterygoid fossae deeply excavated above level of molar alveoli. Stapedial foramen large or very small (entirely occluded in some specimens); other osteological traces of carotid circulation variable. Buccinator-masticatory and accessory

oval foramina separated by vertical strut of alisphenoid. Auditory bullae large or small but always globular, with short bony eustachian tubes. Braincase above bulla on each side perforated by large postglenoid foramen and subsquamosal fenestra separated by slender hamular process of squamosal. Tegmen tympani (petrosal roof of bullar capsule) overlaps posterior margin of squamosal below postglenoid foramen.

Mandible deep (from coronoid process to angle) in proportion to its length; coronoid process strong and falciform; angular process extends posteriorly beyond condyle; lower incisor root contained in prominent capsular process posteroventral to base of coronoid.

Upper incisors smooth or grooved, strongly opisthodont or procumbent and almost orthodont, but enamel bands always deeply pigmented (yellow or orange, never whitish). Upper molar rows parallel or slightly convergent; upper molars hypsodont and lophodont, with principal cusps and crests connected in more-or-less continuous sigmoidal series. Anterocone of M1 undivided; anteroloph absent as a discrete structure on M1, present and well developed on M2 and M3; mesoloph absent on all upper teeth; posteroloph absent (or fused with metacones) on all upper teeth; M1 with four roots, M2 and M3 each with three roots. Anteroconid of m1 undivided; anterolophid and mesolophid absent on all lower teeth; posterolophid well developed on m1 and m2, absent (or fused with entoconid) on m3; m1 with three or four roots, m2 and m3 each with three roots.

Axial skeletal elements exhibiting little variation in number, with modal counts of 12 ribs, 19 thoracicolumbar vertebrae, 4 sacral vertebrae, and 23 to 25 caudal vertebrae in all available species samples. First rib articulates with seventh cervical and first thoracic vertebrae; greatly elongated neural spine on second thoracic vertebra; entepicondylar foramen of humerus absent.

Stomach unilocular and hemiglandular (Carleton, 1973); gall bladder present (Voss, 1991: table 4); male accessory secretory organs consisting of one pair each of bulbourethral, anterior and dorsal prostate, ampullary and vesicular glands, and two pairs each of preputials and ventral prostates (Voss and Linzey, 1981); glans penis complex, with tri-

digitate bacular cartilage and deep terminal crater containing three bacular mounds, one dorsal papilla, lateral papillae, and a bifurcate urethral flap (Hooper and Musser, 1964).

CONTENTS: Sixty-nine Recent species-group taxa are referred to the genus; 57 of these, from North and Central America, may represent only seven valid species (*alleni*, *arizonae*, *fulviventer*, *hispidus*, *leucotis*, *mascoensis*, and *ochrognathus*; see Hall, 1981), but the Central American "subspecies" of *hispidus* have never been critically revised. The twelve remaining nominal taxa, based on South American specimens, represent four diagnosable species as shown below. Martin (1979) reviewed the fossil record of *Sigmodon*, which includes many nominal Pleistocene forms.

PHYLOGENETIC RELATIONSHIPS

Despite its extensive North American distribution, *Sigmodon* has usually been compared with several genera endemic to South America, *Holochilus*, *Reithrodon*, and *Neotomys*, the four together constituting the "sigmodont" group of Hershkovitz (1955). Despite certain resemblances in zygomatic architecture and molar occlusal morphology noted by Thomas (1894), Ellerman (1941), Sanborn (1947), and Hershkovitz (1955), however, these genera diverge in other characters and their relationships are not well understood. In comparisons of penis morphology, *Reithrodon* and *Holochilus* differ strikingly from *Sigmodon* but resemble members of other suprageneric groups of Neotropical muroids: Hooper and Musser (1964) emphasized similarities between *Reithrodon* and some phyllotines, and between *Holochilus* and oryzomyines. The glans penis of *Neotomys* has not been described.

The standard (unbanded) karyotypes of *Reithrodon* and *Neotomys* resemble those of some phyllotines (Pearson and Patton, 1976) but Gardner and Patton (1976: 31–32) also noted chromosomal similarities with *Sigmodon* and suggested that *Neotomys* "... could be annectant between the phyllotines and the sigmodonts." Some standard karyotypes of *Holochilus brasiliensis* (sensu Hershkovitz, 1955) closely resemble those both of *Sigmodon* and *Oryzomys* species

(Gardner and Patton, 1976), but Baker et al.'s (1983) analysis of *G*-banded chromosomes purported to demonstrate that *H. brasiliensis* is more closely related to *Oryzomys* than to *Sigmodon*.

As a consequence of these and other anatomical and cytological comparisons, Reig (1984, 1986) and Olds and Anderson (1989) placed *Reithrodon* and *Neotomys* in the Phyllotini, but the latter authors cautioned that tribal monophyly is not unambiguously supported by character data. Reig (1984, 1986) classified *Holochilus* and *Sigmodon* as the only members of the (undiagnosed) tribe Sigmodontini, but Voss (1991) pointed out that the derived absence of a gall bladder only in the former genus supports Hooper and Musser's suggestion of oryzomyine affinities.

These ambiguous and conflicting observations about relationships are typical of the unsatisfactory current state of knowledge concerning Neotropical muroid systematics emphasized by Carleton and Musser (1989: 53–55). Acknowledging that ambiguity and controversy exist is frustrating but salutary: we should recognize the need for remedial research and admit that phylogenetic assumptions current in the literature may be wrong. Unfortunately, the widespread use of formal nomenclature for suprageneric groups of Neotropical muroids (e.g., Akodontini, Ichthyomyini, Oryzomyini, Phyllotini, Scaptheromyini, Sigmodontini) conveys no such healthy skepticism. Despite Reig's (1980: 262) conviction that most South American muroids "... show a clear-cut pattern of intergeneric affinity, as revealed by various organ-systems and by chromosomes," the monophyly of only one of the above-named tribes is unambiguously supported by shared, derived attributes (Voss, 1988).

The phylogenetic relationships of *Sigmodon* are unknown, and the systematic context within which alternative hypotheses must be evaluated is daunting. The lack of convincing synapomorphies for any group of New World muroids that includes the genus, even the subfamily Sigmodontinae (Carleton and Musser, 1984), necessitates sampling representative Old World taxa as outgroups for any cladistic analysis that merits serious consideration. Quite possibly, significant future progress at this level of muroid phylogenetics

will devolve to molecular comparisons. Aspects of systematic sampling design for testing biogeographically relevant hypotheses of relationships with *Sigmodon* are discussed in the concluding section of this report.

VARIATION WITHIN AND AMONG THE SOUTH AMERICAN SPECIES

The South American forms of *Sigmodon* recognized as valid in this report, *hispidus*, *alstoni*, *peruanus*, and *inopinatus*, can all be identified by the morphological criteria described below. Although qualitative characters are sufficient for the simple purpose of diagnosis, analyses of morphometric data provide additional evidence of phenotypic divergence and reinforce the biological conclusion that four species are represented among the specimens examined. Some characters of traditional taxonomic interest but of little real value in the present context are also treated here for the sake of descriptive completeness.

QUALITATIVE EXTERNAL CHARACTERS

South American *Sigmodon* are remarkably uniform in external appearance. No interspecific variation is apparent in the distribution of vibrissae, the number of plantar tubercles, or any gross aspects of the ears, feet, and tail. Females of *hispidus*, *alstoni*, and *peruanus* consistently have ten teats in five pairs (inguinal, abdominal, thoracic, postaxial, and pectoral), but mammae number may differ in *inopinatus*: one specimen (AMNH 66308) has ten teats, but the thoracic pair is apparently absent in six other mature females of this rare species. With this exception, qualitative variation in external features is limited to pelage density, texture, and pigments.

Pelage density and texture are correlated with altitude: specimens from lower elevations have close, thin, coarse fur, whereas specimens from higher elevations have deeper, denser, and softer pelts. This ecomorphological correlation can be observed both within species (e.g., by comparing specimens of *alstoni* from Hato El Frío, at 60 m in the Llanos, with those from Arabopó, at 1300 m in the Gran Sabana), and between *inopinatus* (endemic to the high páramos of Andean Ec-

uador) and other South American species (which occur at much lower altitudes). Populations with denser body pelage likewise have more thickly furred ears and tails, an observation that can also be documented by comparisons within species or between *inopinatus* and its lowland congeners.

Pelage pigments vary within all of the widely ranging species of South American cotton rats: *hispidus*, *alstoni*, and *peruanus*. All species exhibit the coarsely grizzled, brownish dorsal pattern characteristic of the genus, but populations differ in overall saturation (of reddish and yellow tones) and darkness. Available ecological information suggests that dramatic contrasts in pelage color among geographic samples are correlated with environmental humidity; an example is provided by the dark specimens of *peruanus* collected from secondary growth in the humid valley of the Río Chimbo (Ecuadorean locality 3) and the pale skins of the same species from arid landscapes in northwestern Peru.

The grizzled pattern of the dorsal body pelage is relieved only by subtle facial markings common to all the South American species, although varying in brightness and definition within and among populations: a patch of clear reddish or yellow fur around the nose, and rings of pale (usually yellow) fur that encircle the eyes. The tails of all South American *Sigmodon* are darker above than below, a pattern that is indistinct in some samples and sharply defined in others of the same species. The long, silvery guard hairs on the rump and flanks of *inopinatus* that Anthony (1924) believed to be diagnostic are present but less conspicuous in other South American species as well.

EXTERNAL DIMENSIONS

South American species of *Sigmodon* do not differ greatly in size, but external measurements of representative samples (table 1) reveal that *alstoni* is appreciably smaller in head-and-body length than *hispidus*, *peruanus*, and *inopinatus*. The smaller size of the former is also evident in hindfoot length, a contrast of practical value for identification where *alstoni* and *hispidus* are sympatric in Colombia and Venezuela. Chipman (1965)

found significant dimorphism in age-controlled sex comparisons of head-and-body length for captive-bred *S. hispidus*, but sex differences in external dimensions are not apparent in the samples treated here.

Ratios of tail and hindfoot to head-and-body length (table 2) suggest that *peruanus* and *inopinatus* have relatively shorter appendages than *hispidus* and *alstoni*, but substantial variability in these proportions within species is evident and several samples are not large. Furthermore, since length of tail is subtracted from total length to obtain length of head-and-body, minor methodological differences among collectors measuring tails could substantially affect the computed ratio LT/HBL. An additional complexity is introduced by ontogenetic variation: body length increases steadily throughout life whereas the tail and hindfeet complete most of their growth in the first few weeks after birth (Jiménez, 1971); therefore, younger adults have relatively longer appendages than older animals, and sample discrepancies in age structure may confound population comparisons of external proportions. In view of these interpretive difficulties, which cannot be addressed with materials currently available, confident taxonomic inferences from the data in table 2 are impossible despite the impressive magnitude of some apparent differences.

QUALITATIVE CRANIODENTAL CHARACTERS

By contrast with the essentially undifferentiated external appearance of South American cotton rats, many aspects of craniodental morphology vary among the groups of populations recognized as species in this report. Qualitative and quantitative character variation in the head skeleton support the same taxonomic assignments, but it is convenient to treat these sources of information separately. The present section summarizes discrete variation, traits that can be scored as either present or absent, together with aspects of shape variation that are more easily described verbally than measured.

Nasal bones: The nasals are long in most species of *Sigmodon*, projecting anteriorly beyond the premaxillae to conceal the strongly opisthodont incisors from dorsal view (fig. 6A, B). *S. inopinatus*, however, has short na-

TABLE 1

Summary Statistics^a for External Measurements (in millimeters) of Adult Specimens of South American *Sigmodon* Species

Species	Length of head-and-body	Length of tail	Length of hindfoot
<i>hispidus</i> ^b	150 ± 14 (125–174)	114 ± 11 (92–135)	33 ± 1 (30–36)
<i>alstoni</i> ^c	137 ± 11 (106–152)	91 ± 8 (72–102)	27 ± 1 (24–29)
<i>peruanus</i> ^d	148 ± 13 (120–172)	93 ± 10 (79–116)	31 ± 2 (28–34)
<i>inopinatus</i> ^e	153 ± 11 (136–167)	88 ± 7 (78–99)	29 ± 1 (28–30)

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).

^b N = 24; sample from Montalbán, Venezuelan locality 18.

^c N = 26; sample from Hato El Frío, Venezuelan locality 6.

^d N = 35; sample from Chongoncito, Ecuadorean locality 11.

^e N = 9; sample from Urbina, Ecuadorean locality 4.

sals that do not project beyond the premaxillae, and the procumbent incisors of this species are consequently exposed when the skull is viewed from a dorsal perspective (fig. 6C, D).

Incisive foramina: The incisive foramina are prominent slots in the diastemal palate that accommodate the soft tissues of the nasopalatine apparatus and communicate the nasopalatine canals (Quay, 1954). Among muroids, these foramina display considerable taxonomic variation in size and shape, the functional significance of which is obscure; South American species of *Sigmodon*, however, only exhibit modest differences in foraminal length. In most specimens of *hispidus* (fig. 7A), the foramina are long, extending posteriorly to or between the molar alveoli (such that a line tangent to the anterior limits of both first molar sockets is also tangent to or intersects one or both foramina); in *peruanus* (fig. 7B), by contrast, the incisive foramina are usually short and do not extend posteriorly to the level of the molar alveoli; *alstoni* and *inopinatus* exhibit greater variability in the posterior limits of these foramina (table 3).

Palatal bridge: The palatal bridge (an anatomical term peculiar to muroid systematics, denoting the hard palate posterior to the diastema) and the foramina it contains provide several important characters for discriminating South American species of *Sigmodon*. The palatal bridge of mature adult specimens of *hispidus* (fig. 7A) is broad and long in the sense defined by Hershkovitz (1962): broad because the distance across the palate between the first upper molars equals

or exceeds the length of either tooth; and long because the mesopterygoid fossa does not extend between the third molars (i.e., the palate is produced behind the molar rows). Anteriorly, at the level of the first and second molars, the palatal bridge of *hispidus* is smooth, but a median keel is sometimes developed posteriorly; when well developed, this keel is sometimes produced as a small median spine on the posterior palatal margin. Shallow posterolateral sulci containing one or more small pits are found between the median keel and the third molars in some specimens of *hispidus*, but in others the posterior palate is smooth and almost devoid of relief. By contrast, the palatal bridge of *peruanus* (fig. 7B) is narrow and short: the distance across the palate between the first molars is less than the length of either tooth, and the mesopterygoid fossa projects between the third molars. The palatal bridge of *peruanus* is also marked by prominent grooves that extend on each side from the incisive foramen to a well-defined posterolateral sulcus. The posterolateral sulci are always separated by a conspicuous median keel that is often produced as a small spine on the posterior palatal margin.

The morphology of the palatal bridge in other South American species of *Sigmodon* is intermediate to the extremes described above. In adult specimens of *alstoni*, the palate is broad (although generally not so broad as in *hispidus*) but the mesopterygoid fossa often extends between the third molars (not so deeply, however, as in *peruanus*); the palatal bridge is usually smooth, lacking a well-defined median keel and deep posterolateral sulci, but a small, blunt spine is usually pres-

TABLE 2
Mean External Proportions for Population Samples of South American *Sigmodon* Species

Samples ^a	N	Ratios	
		LT/ HBL	HF/ HBL
<i>hispidus</i>			
Venezuela			
8. Rancho Grande	11	0.86	0.24
18. Montalbán	24	0.76	0.22
<i>alstoni</i>			
Venezuela			
6. Hato El Frío	25	0.67	0.20
8. Rancho Grande	15	0.77	0.22
39. San Antonio Maturín	12	0.74	0.23
<i>peruanus</i>			
Ecuador			
3. Puente de Chimbo	11	0.56	0.20
11. Chongoncito	35	0.63	0.21
13. San Ramón	17	0.69	0.21
<i>inopinatus</i>			
Ecuador			
1. Las Cajas	3	0.55	0.19
4. Urbina	9	0.58	0.19

^a Named and numbered as in the gazetteer.

ent on the posterior palatal margin. Few specimens of *inopinatus* are available, but most intact adult skulls have narrow, short palates (though neither so narrow or as short as in *peruanus*); the palate lacks deep longitudinal grooves and well-defined posterolateral sulci, but a distinct median keel between the third molars is always produced as a small, sharp spine on the posterior palatal margin.

Posterior palatal foramina: The posterior palatal foramina are small perforations in the palatal bridge, one on each side, at about the level where the second and third molars abut. In *alstoni* and *peruanus*, these foramina are always contained in the maxillary-palatine suture, and this is also the usual condition for specimens of *inopinatus*; in *hispidus*, however, the posterior palatal foramina are often enclosed completely by the palatine bones (table 4).

Stapedial circulation: Two morphologies of the stapedial arterial circulation are present among South American species of *Sigmodon*, and both can be recognized by osteological features. The stapedial pattern

TABLE 3
Relative Frequencies of Alternative Morphologies of the Incisive Foramina in South American *Sigmodon* Species

Morphology ^a	Species samples			
	<i>hispidus</i> (N = 142)	<i>alstoni</i> (N = 67)	<i>peruanus</i> (N = 100)	<i>inopinatus</i> (N = 11)
short	0.05	0.28	0.95	0.18
intermediate	0.13	0.24	0.04	0.09
long	0.82	0.48	0.01	0.73

^a Key: short, incisive foramina do not extend to or between molar alveoli; intermediate, incisive foramina extend to but not between molar alveoli; long, incisive foramina extend between molar alveoli.

widely recognized as primitive for muroids (e.g., by Bugge, 1970; Carleton, 1980; and Voss, 1988) occurs only in *peruanus*. Every specimen of that species has a large stapedial foramen in the petrotympanic fissure on the posteromedial surface of the bulla; the stapedial artery enters the bullar capsule through this orifice, passes through the stapes, and exits the bulla through a cleft in the tegmen tympani. Inside the braincase, the stapedial artery divides into supraorbital and infraorbital branches, and the former vessel leaves a prominent groove along the inner surfaces of the squamosal and alisphenoid bones as it passes rostrally to enter the orbit through a large sphenofrontal foramen (see Carleton, 1980; Voss, 1988; and Carleton and Musser, 1989 for illustrations of this plesiomorphic condition). In all other species of *Sigmodon*, the stapedial artery is extremely small and probably supplies only the middle ear and some of the meningeal circulation; the sta-

TABLE 4
Relative Frequencies of Alternative Morphologies of the Posterior Palatal Foramina in South American *Sigmodon* Species

Morphology ^a	Species samples			
	<i>hispidus</i> (N = 136)	<i>alstoni</i> (N = 69)	<i>peruanus</i> (N = 100)	<i>inopinatus</i> (N = 11)
P/M	0.24	1.00	1.00	0.82
P	0.76	0.00	0.00	0.18

^a Key: P/M, posterior palatal foramina in the maxillary/palatine suture; P, foramina enclosed by palatines.

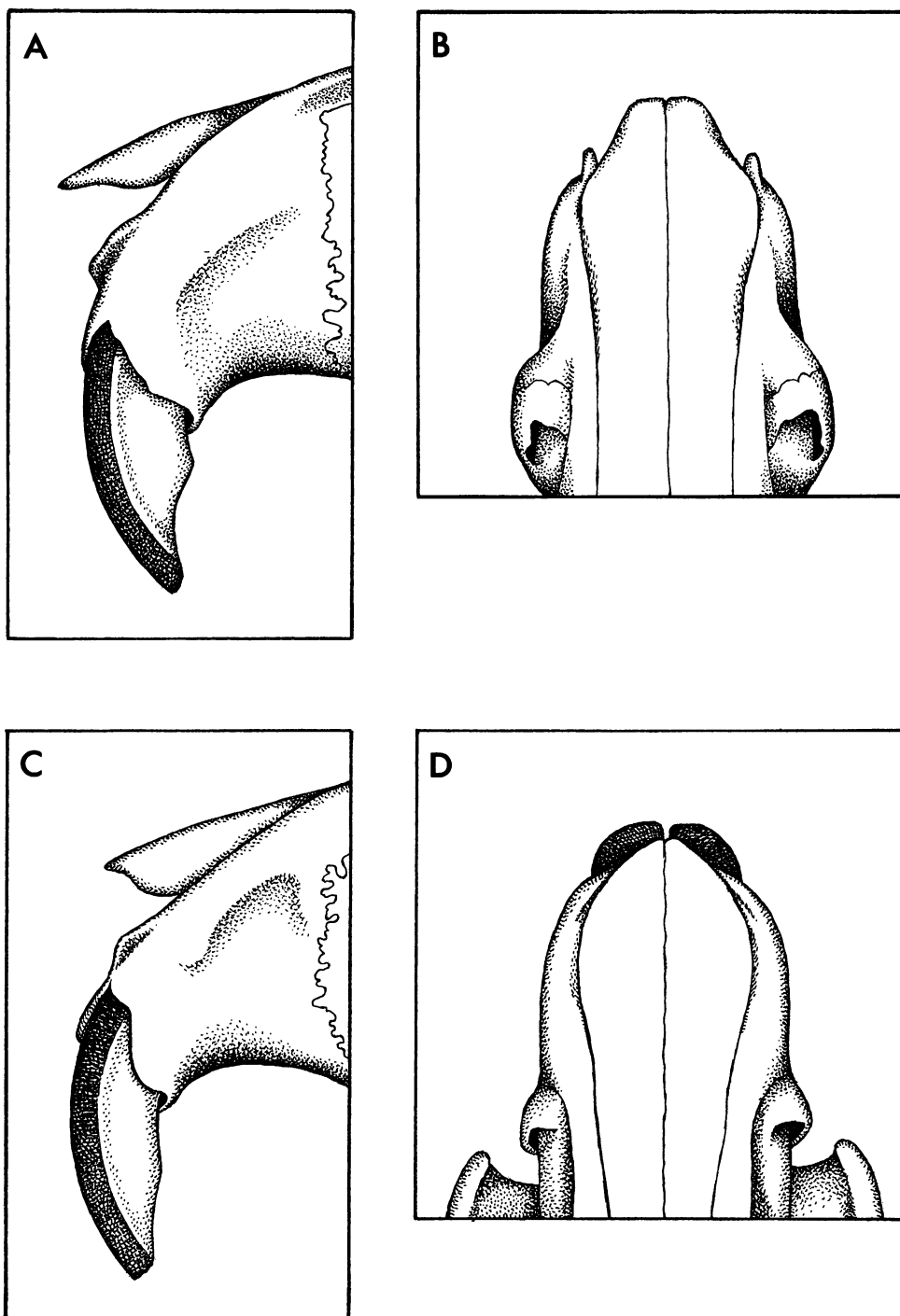


Fig. 6. Dorsal and lateral views of the rostrum. A, B, *Sigmodon peruanus* (AMNH 67042); C, D, *S. inopinatus* (AMNH 66308).

pedial foramen is then reduced to a minute pore (which appears to be entirely occluded in some specimens), while the squamosal-

alisphenoid groove and sphenofrontal foramen are both absent. The facial (ophthalmic and internal maxillary) circulation in this de-

rived condition is instead supplied by a branch of the internal carotid (anastomosis A5 in Bugge's terminology; op. cit.) which leaves a diagonal, internal groove across the roof of the parapterygoid fossa that is sometimes visible externally as a streak of translucent bone (see fig. 21A in Carleton and Musser, 1989).

Auditory bullae: The auditory bullae are small in *hispidus* (fig. 8A), *alstoni*, and *inopinatus*, but conspicuously larger and more inflated in *peruanus* (fig. 8B).

Incisors: The upper incisors of *hispidus* and *peruanus* are smooth and strongly opisthodont (not remarkably different from the common morphology of these teeth in many other Neotropical muroid genera) and differ only by their relative width, the incisors of *hispidus* being visibly narrower than those of *peruanus* when skulls of like size are compared. The upper incisors of *inopinatus* are also smooth, but are noticeably more procumbent than those of *hispidus* and *peruanus* (fig. 6); in no specimen of *inopinatus*, however, are the incisors actually orthodont.

The deeply grooved upper incisors of *alstoni* (fig. 9B) were the basis for the original assignment of that species to the genus *Reithrodon* (by Thomas, 1880), and provide the only criterion for separating *Sigmomys* from *Sigmodon*. The grooves, which divide the enameled anterior surface of the tooth into unequal medial and lateral moieties, are always distinct and in no population sample that I have examined is there any evidence that grooves are subject to polymorphic variation (as implied by Hershkovitz, 1955). Where groove-toothed and smooth-toothed *Sigmodon* have been collected together they differ by other characters as well and sympatry, not polymorphism, is the biologically appropriate interpretation (see the species account for *alstoni* below).

Molar occlusal morphology: Differences in molar occlusal design among *Sigmodon* species are generally subtle, but the maxillary dentition of *peruanus* diverges from the morphology common to other South American congeners. In *hispidus*, *alstoni*, and *inopinatus* (fig. 10A, B, D) the protocone and paracone are opposite one another (or very nearly so), as are the hypocone and metacone, and the cusp apices are obtusely rounded. In *peruanus* (fig. 10C), however, lingual and la-

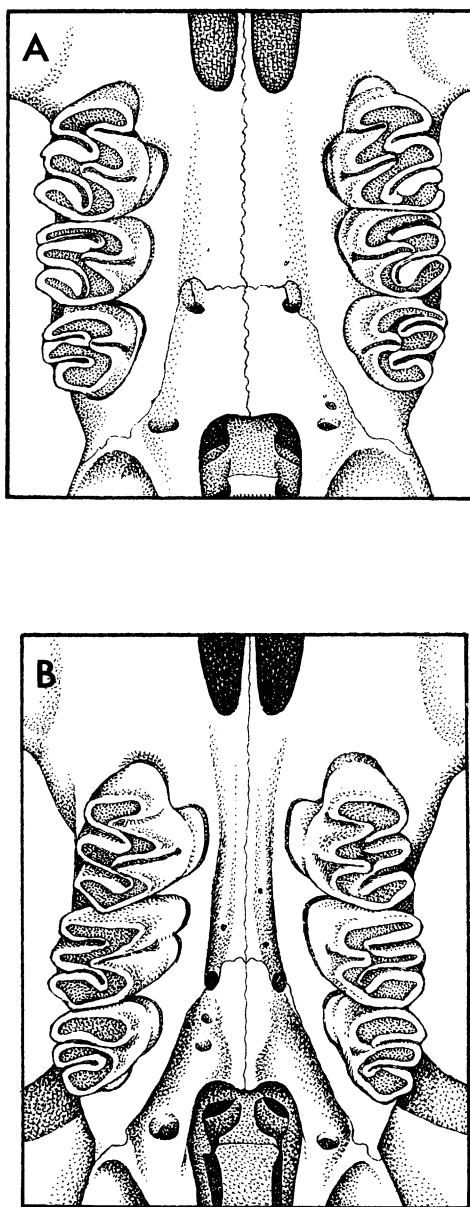


Fig. 7. Morphology of the posterior palate. A, *Sigmomys hispidus* (USNM 442531); B, *S. peruanus* (AMNH 67028).

bial cusps alternate down the long axis of the toothrow, and their angular shapes (especially when unworn) recall the prismatic divisions of microtine molars. Interspecific comparisons of mandibular toothrows (fig. 11) reveal similar if less conspicuous patterns.

Lower first molar roots: The anteriormost mandibular molar exhibits significant vari-

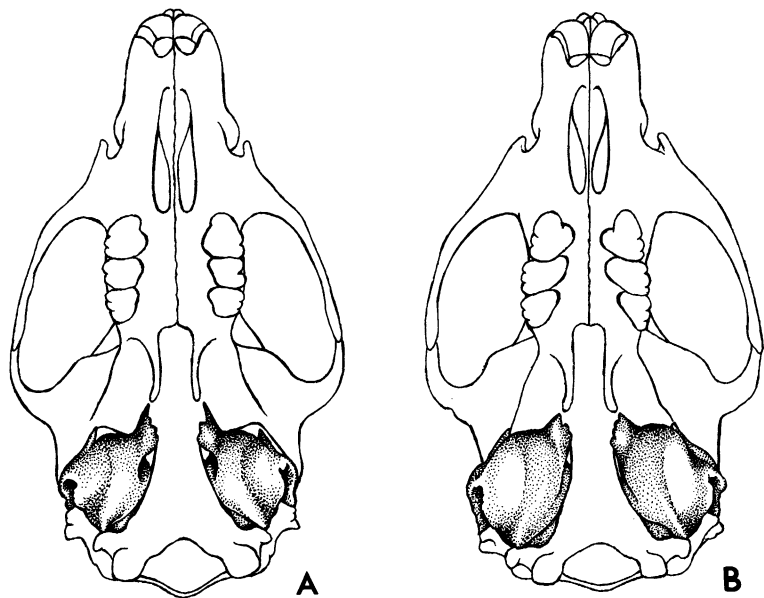


Fig. 8. Relative size of the auditory bullae. A, *Sigmodon hispidus* (USNM 442531); B, *S. peruanus* (AMNH 67028).

ation in root number among *Sigmodon* species, and Martin (1979) used this character as the primary basis for assigning Recent and Pleistocene forms to species groups. A large anterior root (under the anteroconid), a large posterior root (under the hypoconid-entoconid pair), and a smaller labial root (under the protoconid) are always present; the variable element is lingual. The lingual root is well developed (but always smaller than the anterior and posterior roots) in most examples of *hispidus* and *inopinatus*; in *alstoni* and *peruanus*, however, the lingual root is either absent (the commonest condition), or it is very small and weak, a slender thread of den-

tine that may be hard to see above the alveolus (table 5). Because molar roots are often difficult to observe in young specimens whose teeth are deeply embedded in alveolar bone, root numbers are best determined from older individuals.

CRANIODENTAL DIMENSIONS

Age-correlated growth and sexual dimorphism are the most important tangible causes of morphometric variation within the field-collected, mixed cross-sectional samples ordinarily available for systematic studies of mammals. The effects of postweaning growth and sex on muroid craniodental measurement variation were recently analyzed by Voss et al. (1990) and Voss and Marcus (in press) who discovered that the first principal component of the within-sample covariance matrix (of log-transformed measurements) approximates a general size factor with coefficients that reflect ontogenetic allometry. Within samples, specimen scores on general size are correlated with age (and sometimes also with sex), but variation residual to the first principal component is essentially age- and sex-invariant. An important implication of these results is that estimates of Mahalanobis distances, and of sample mean differ-

TABLE 5
Relative Frequencies of Alternative Conditions of the Lingual Root of m1 in South American *Sigmodon* Species

Morphology	Species samples			
	<i>hispidus</i> (N = 52)	<i>alstoni</i> (N = 50)	<i>peruanus</i> (N = 75)	<i>inopinatus</i> (N = 11)
well developed	0.73	0.00	0.04	0.91
small and weak	0.23	0.24	0.31	0.09
absent	0.04	0.76	0.65	0.00

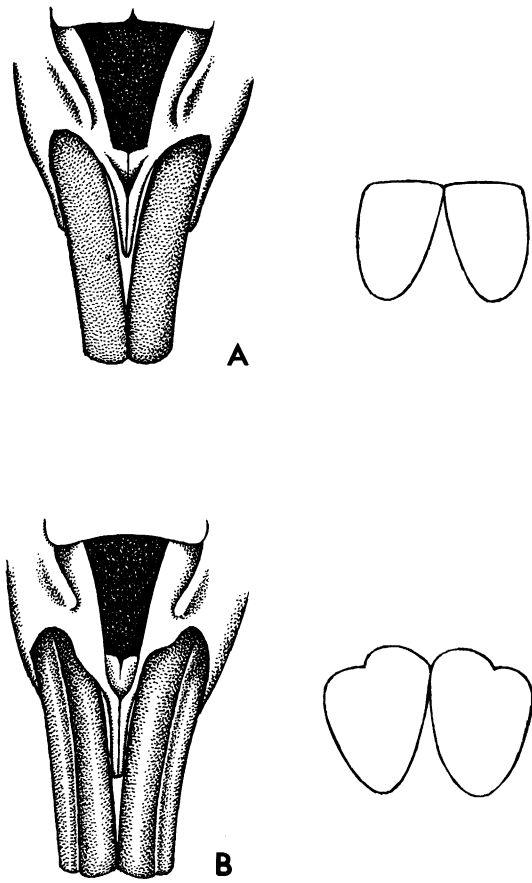


Fig. 9. Upper incisors. A, *Sigmodon hispidus* (USNM 442508); B, *S. alstoni* (USNM 520676).

ences adjusted for general size (see Materials and Methods: Multivariate Statistics), are insensitive to minor sample discrepancies in age and sex composition.

Samples and sexual dimorphism: The samples employed in the following analyses (table 6) consist of “adults” as defined in Materials and Methods, but a considerable ontogenetic range is obviously represented in each (the development of cranial ridges and crests increases with age and provides a subjective basis for this judgment; see Chipman, 1965). Summary univariate statistics for the sample of *Sigmodon hispidus* from Florida are tabulated by gender (table 7), but univariate statistics for other samples (which appear in tables accompanying the taxonomic accounts) are not. Males usually average larger than females, but sex differences are always small by comparison with the interspecific con-

TABLE 6
Population Samples of *Sigmodon* Species Included in Morphometric Analyses

Samples ^a	N
<i>hispidus</i>	
United States	
Lake Placid, Florida	37
Colombia	
12. Valle de Suaza	37
14. Minca	28
Venezuela	
8. Rancho Grande	14
18. Montalbán	40
<i>alstoni</i>	
Guyana	
2. Kanuku Mountains	14
Venezuela	
6. Hato El Frío	16
8. Rancho Grande	26
39. San Antonio Maturín	12
<i>peruanus</i>	
Ecuador	
3. Puente de Chimbo	12
11. Chongoncito	16
13. Isla Puná	34
<i>inopinatus</i>	
Ecuador	
4. Urbina	8

^a Named and numbered as in the gazetteer.

trasts of primary interest here. All of the analyses reported below are therefore of sample data unadjusted for sex.

Mahalanobis distances: Although Mahalanobis distances between some samples judged to be conspecific by qualitative criteria are large, interspecific distances are consistently greater (fig. 12). The Florida population representing the typical morphology of *hispidus* is the most divergent among the five samples referred to that species, but the clusters identified as *peruanus* and *alstoni* are not significantly more homogeneous despite the less extensive geographic ranges they represent. The type series of *inopinatus* (from Urbina) is clearly divergent from all other samples of South American *Sigmodon* for which sufficient measurement data are available for analysis.

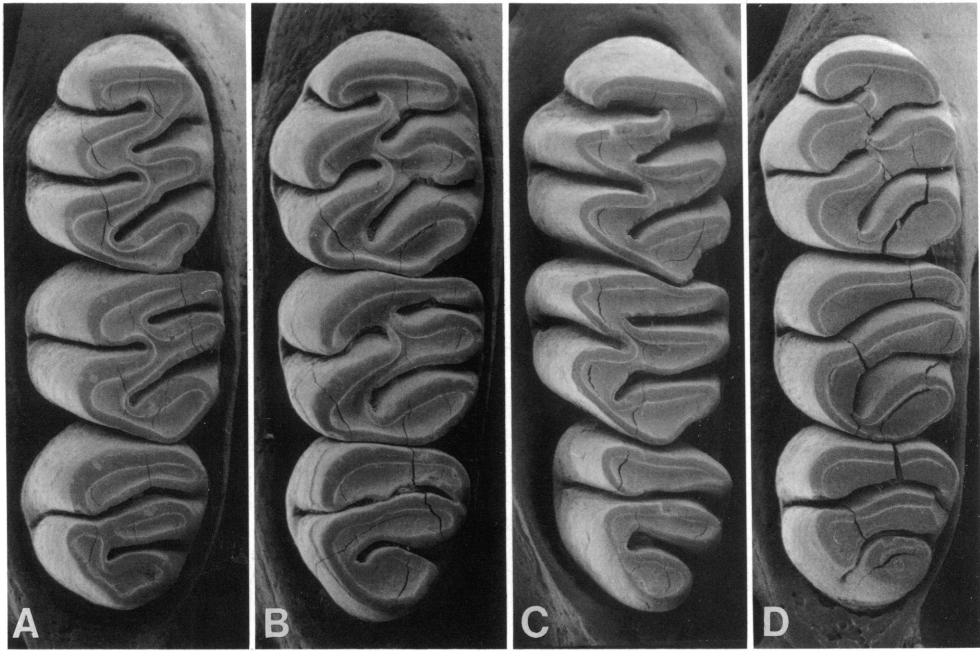


Fig. 10. Left maxillary molar series of South American *Sigmodon* species. A, *S. hispidus* (USNM 542133); B, *S. alstoni* (MHNLS 8218); C, *S. peruanus* (AMNH 63015); D, *S. inopinatus* (AMNH 66312).

Although these results provide unambiguous evidence that taxa distinguishable by qualitative traits also differ in quantitative aspects of craniodental morphology, no explicitly phylogenetic interpretation of the illustrated branching pattern is possible. This limitation arises from the difficulty of distinguishing primitive from derived similarity in

measurement data, and because morphometric divergence cannot be assumed to proceed at a constant rate in all lineages. The higher-order branching (among species), which occurs over a fairly narrow range of distance values, is especially unlikely to have any historical significance. Some of the clusters of populations identified as species in

TABLE 7
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Sigmodon hispidus* from 8 mi S Lake Placid, Florida

	Females (N = 20)	Males (N = 17)	Whole sample
CIL	29.7 ± 2.1 (26.4–34.1)	30.5 ± 3.2 (26.4–35.5)	30.1 ± 2.7
LD	8.1 ± 0.8 (6.9–9.7)	8.5 ± 1.3 (6.8–10.7)	8.3 ± 1.1
LM	6.4 ± 0.2 (6.0–6.8)	6.4 ± 0.3 (6.0–6.9)	6.4 ± 0.2
BM1	2.1 ± 0.1 (1.9–2.2)	2.1 ± 0.1 (2.0–2.3)	2.1 ± 0.1
LIF	6.9 ± 0.6 (6.0–8.2)	7.1 ± 0.9 (5.7–8.6)	7.0 ± 0.8
BR	5.2 ± 0.3 (4.6–5.8)	5.4 ± 0.6 (4.4–6.7)	5.3 ± 0.5
BPB	2.5 ± 0.3 (1.9–3.0)	2.5 ± 0.4 (2.0–3.3)	2.5 ± 0.4
BZP	3.4 ± 0.3 (2.7–4.0)	3.4 ± 0.5 (2.7–4.4)	3.4 ± 0.4
LIB	4.8 ± 0.3 (4.4–5.4)	4.8 ± 0.3 (4.4–5.4)	4.8 ± 0.3
DI	1.7 ± 0.2 (1.4–2.0)	1.8 ± 0.2 (1.4–2.0)	1.7 ± 0.2
BIT	2.4 ± 0.3 (1.9–2.8)	2.4 ± 0.3 (1.8–3.0)	2.4 ± 0.3
ZB	18.3 ± 1.0 (16.4–20.2)	18.6 ± 1.5 (16.4–21.0)	18.5 ± 1.3

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).

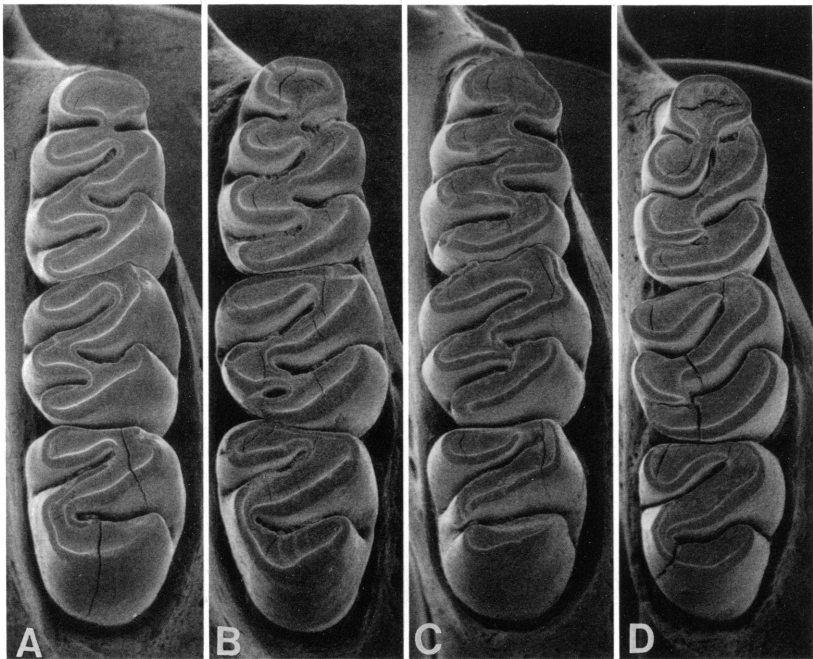


Fig. 11. Right mandibular molar series of South American *Sigmodon* species. Species and specimens are the same as those in fig. 10.

figure 12 may be monophyletic, but this analysis by itself does not provide a sufficient basis for inferring monophyly.

General size and species differences: Gen-

eral size coefficients estimated from the largest South American sample of each species (table 8) reveal strikingly similar patterns of multivariate allometric growth. Isometry for

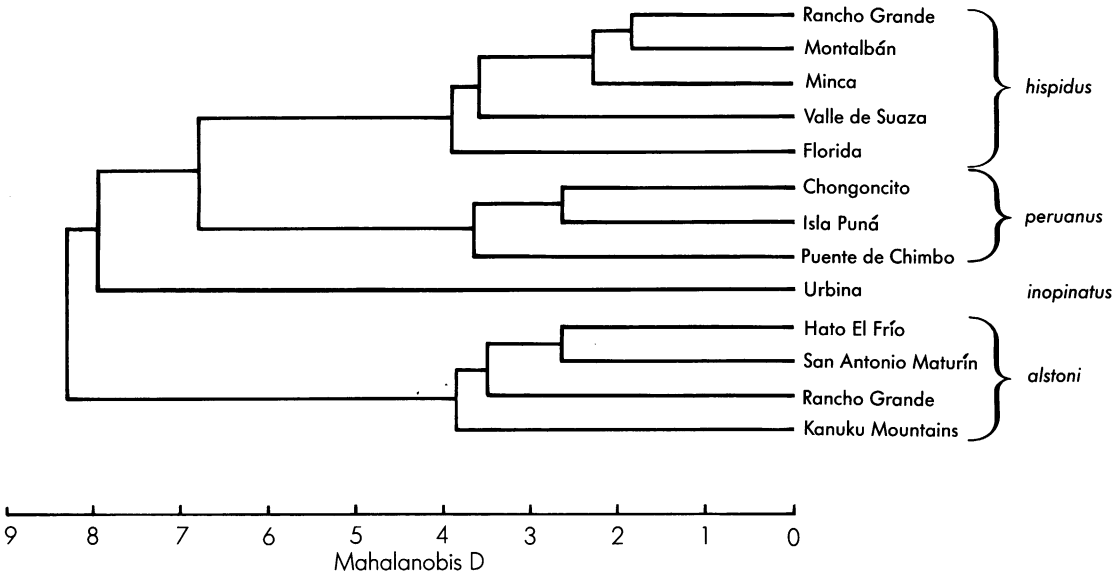


Fig. 12. UPGMA clustering of Mahalanobis distances among 13 population samples of *Sigmodon* species. The units of Mahalanobis distance, along the horizontal, are within-sample standard deviations adjusted for measurement covariance. Sample sizes and gazetteer references are provided in table 6.

TABLE 8

General Size Coefficients of Log-Transformed Measurements for Four Samples of South American *Sigmodon* Species

	<i>hispidus</i> ^a (N = 40)	<i>alstoni</i> ^b (N = 26)	<i>peruanus</i> ^c (N = 34)	<i>inopinatus</i> ^d (N = 8)
CIL	0.24	0.24	0.27	0.23
LD	0.34	0.33	0.35	0.36
LM	0.00	0.10	0.03	0.02
BM1	0.02	0.12	0.02	0.06
LIF	0.31	0.29	0.30	0.28
BR	0.25	0.20	0.28	0.20
BPB	0.54	0.41	0.42	0.59
BZP	0.25	0.40	0.45	0.30
LIB	0.11	0.18	0.11	0.10
DI	0.36	0.29	0.27	0.30
BIT	0.38	0.45	0.36	0.36
ZB	0.17	0.20	0.21	0.16

^a Sample from Montalbán, Venezuelan locality 18.

^b Sample from Rancho Grande, Venezuelan locality 8.

^c Sample from Isla Puná, Ecuadorean locality 13.

^d Sample from Urbina, Ecuadorean locality 4.

these data is indicated by normalized coefficients about equal to 0.29 (i.e., the inverse square-root of the number of variables, see Jolicoeur, 1963); measurement variables with coefficients much smaller than this value exhibit negative allometry, whereas variables with much larger coefficients exhibit positive allometry. In conformity with results previously reported for other muroids (Voss, 1988; Voss et al., 1990; Voss and Marcus, in press), molar measurements (LM, BM1), interorbital breadth (LIB), and measurements that span the braincase (ZB in this study), have consistently smaller coefficients than diastemal length (LD), palatal breadth (BPB), and breadth across the incisor tips (BIT). Therefore, small (and usually young) specimens have disproportionately larger molars and neurocrania, but smaller rostra, and narrower palates and incisors by comparison with larger (and usually older) specimens in the same sample. Comparisons between samples must be adjusted for these ontogenetic allometries in order to identify age-invariant aspects of interspecific shape differences.

Mean sample differences adjusted for general size in separate analyses of covariance (table 9) reveal diverse morphometric contrasts between *Sigmodon hispidus* and the other South American species that have

TABLE 9

Interspecific Differences Adjusted for General Size^a in Twelve Log-Transformed Craniodental Measurements

	Between <i>Sigmodon hispidus</i> and		
	S. <i>alstoni</i>	S. <i>peruanus</i>	S. <i>inopinatus</i>
CIL	-0.08	0.14	0.07
LD	0.11	0.04	0.09
LM	-0.72	0.27	0.19
BM1	-0.32	0.18	0.23
LIF	-0.13	-0.33	-0.14
BR	-0.30	0.15	0.15
BPB	0.12	-0.63	-0.41
BZP	0.06	0.31	0.27
LIB	-0.37	-0.10	-0.67
DI	0.02	0.28	0.02
BIT	0.30	0.39	0.37
ZB	-0.13	0.08	0.18

^a Tabulated values are mean differences among the species samples listed in the footnotes to table 8, adjusted for general size in separate analyses of covariance, and normalized (so that the sum of the squared coefficients in each column equals unity). Coefficients are signed to indicate divergence from *Sigmodon hispidus*. Specimen scores on these factors are plotted along the vertical axes of figures 13, 14, and 15.

sometimes been synonymized with it. At constant general size, *alstoni* differs most conspicuously by its smaller molar dimensions (LM, BM1) and narrower interorbit (LIB); of the few positive coefficients for this comparison, only the value for BIT is noteworthy, indicating the relatively broader incisors of this generally smaller species. The largest general-size-adjusted coefficients contrasting *peruanus* and *hispidus* describe the much narrower palate (BPB), shorter incisive foramina (LIF), and broader incisors (BIT) of the former. Adjusted for general size, *inopinatus* has a much narrower interorbital region (LIB), narrower palate (BPB), and broader incisors (BIT) than *hispidus*. These inferences from statistical computations can be visually confirmed by inspection of the cranial photographs that accompany the species accounts below.

General size and general-size-adjusted difference factors provide biologically interpretable axes for ordinating specimens. For each of the pairwise species comparisons discussed in the preceding paragraph, specimen

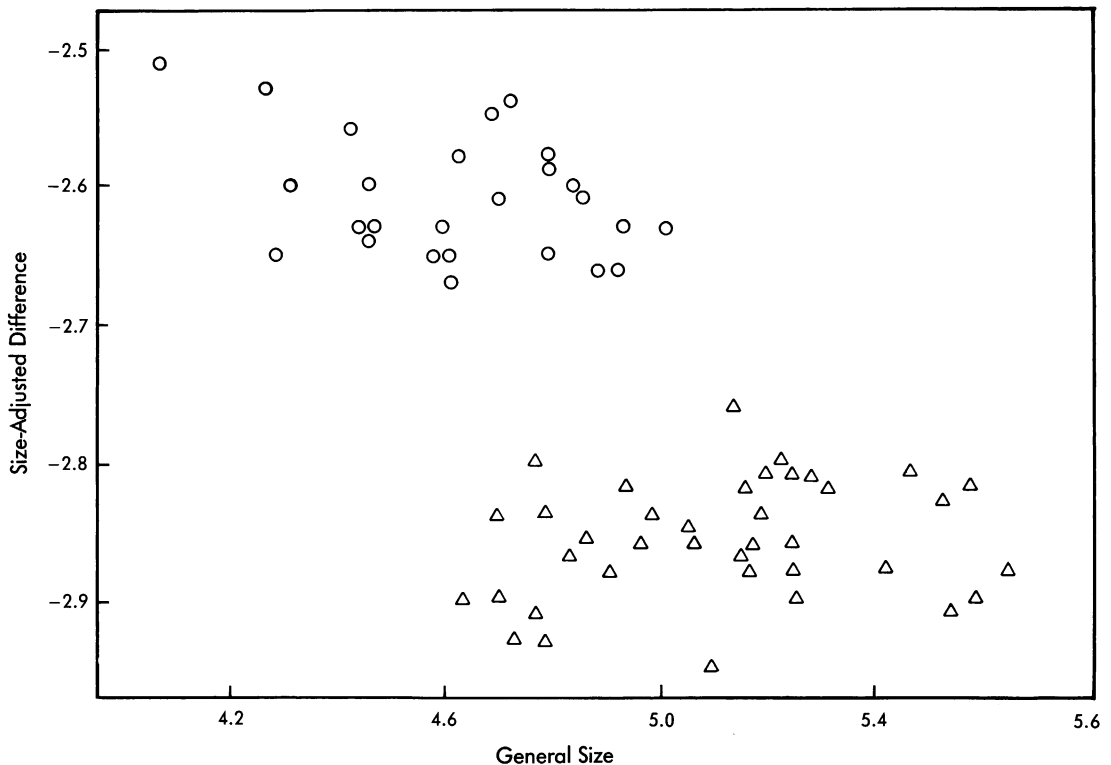


Fig. 13. Specimen scores of *Sigmodon hispidus* (open triangles, from Venezuelan locality 18) and *S. alstoni* (open circles, from Venezuelan locality 8) on factors representing general size and general-size-adjusted differences. Overlapping observations (conspecific specimens with the same factor scores) are not plotted separately.

scores illustrate broadly overlapping general-size distributions, but divergence in general-size-adjusted (age-invariant) aspects of shape variation provides a compelling basis for discrimination (figs. 13, 14, 15). Although other pairwise ordinations (among samples of *alstoni*, *peruanus*, and *inopinatus*) are not documented here, the Mahalanobis distances summarized earlier (in fig. 12) are sufficient to support the conclusion that their multivariate dispersions are likewise discrete.

SPECIES ACCOUNTS

The following accounts provide synonyms, information about type specimens, summaries of geographic distributions, lists of diagnostic characters, congeneric comparisons, descriptions of geographic variation, and comments on taxonomic problems that remain to be solved. Character states listed in the Morphological Diagnosis for each spe-

cies are defined in the preceding section of this report. Only South American taxa are listed in the synonymy for *Sigmodon hispidus*; North American and Central American synonyms are given by Hall (1981). Holotypes of every South American species-group taxon except *hirsutus* were examined in the course of this study; these and other specimens from which I recorded data are listed at the conclusion of each account.

Sigmodon hispidus Say and Ord (Figures 3–5, 7–11, 16, 17)

Sigmodon hispidus Say and Ord, 1825: 354.

Lasiomys hirsutus Burmeister, 1854: 16.

Lasiuromys hirsutus Giebel, 1857: caption to plate 5, figure 1 (an inadvertent misuse of *Lasiuromys* Deville for Burmeister's species according to Winge, 1941: 153)

Isothrix hirsutus Trouessart, 1880: 178.

Sigmodon bogotensis J. A. Allen, 1897b: 121.

Sigmodon sanctaemartae Bangs, 1898: 189.

Sigmodon hirsutus Thomas, 1914: 413.

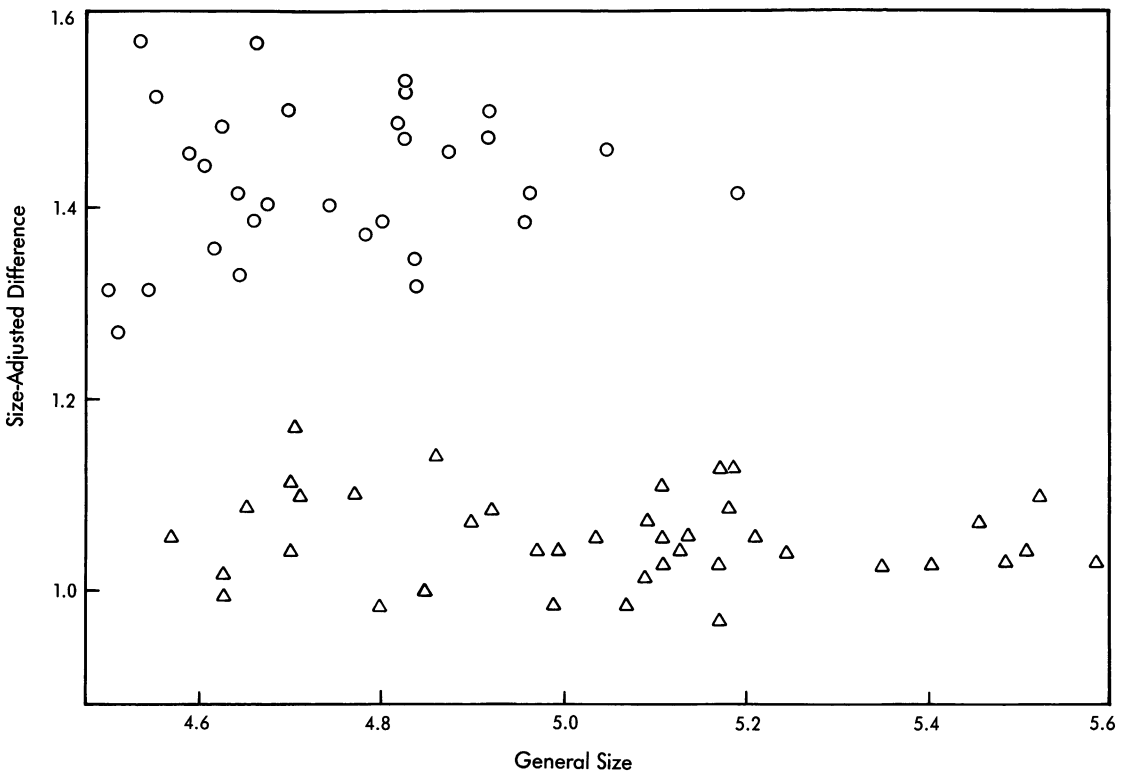


Fig. 14. Specimen scores of *Sigmodon hispidus* (open triangles, from Venezuelan locality 18) and *S. peruanus* (open circles, from Ecuadorean locality 13) on factors representing general size and general-size-adjusted differences. Overlapping observations (conspecific specimens with the same factor scores) are not plotted separately.

Sigmodon hispidus bogotensis Cabrera, 1961: 508.
Sigmodon hispidus hirsutus Cabrera, 1961: 508.

TYPE: Not extant, as explained earlier for the genus.

DISTRIBUTION AND SYMPATRY: From about 41°N in the United States, southward through Mexico and Central America (see Hall, 1981) to South America. In South America, *hispidus* occurs in natural or anthropogenic non-forest habitats below about 3000 m elevation from the Caribbean coast of Colombia southward throughout the entire catchment of the Río Magdalena,⁴ and eastward in coastal lowlands and sierras at least as far as Curupao (66°38'W) in Estado Miranda, Venezuela; south of the coastal sierras, *hispidus* is known from the northwestern Llanos in the Vene-

zuelan states of Barinas, Cojedes, Carabobo, and Guárico. The species is unknown from the Recent fauna of any Caribbean island, but Hooijer (1967) reported Pleistocene remains of "*Sigmodon* cf. *hispidus*" from Aruba.

The geographic ranges of *hispidus* and *alstoni* overlap from extreme northeastern Colombia (in the western foothills of the Serranía de Perijá) eastward to the low mountains surrounding Lago Valencia in Venezuela, and southward into the northwestern Llanos, perhaps as far as the Río Apure. The two species have been collected sympatrically at El Limón and Guamita (both near Venezuelan locality 8), at Camp Rangel (Venezuelan locality 9), at El Trompillo (Venezuelan locality 16), and at Hato Itabana (Venezuelan locality 21).

MORPHOLOGICAL DIAGNOSIS: A large species of *Sigmodon* distinguishable from other South American congeners by its long nasal

⁴ Cuervo Díaz et al. (1986) also reported *hispidus* from the valleys of the Río Cauca and the Río Patía in Colombia, but I have not seen specimens from either region and none are cited elsewhere in the literature.

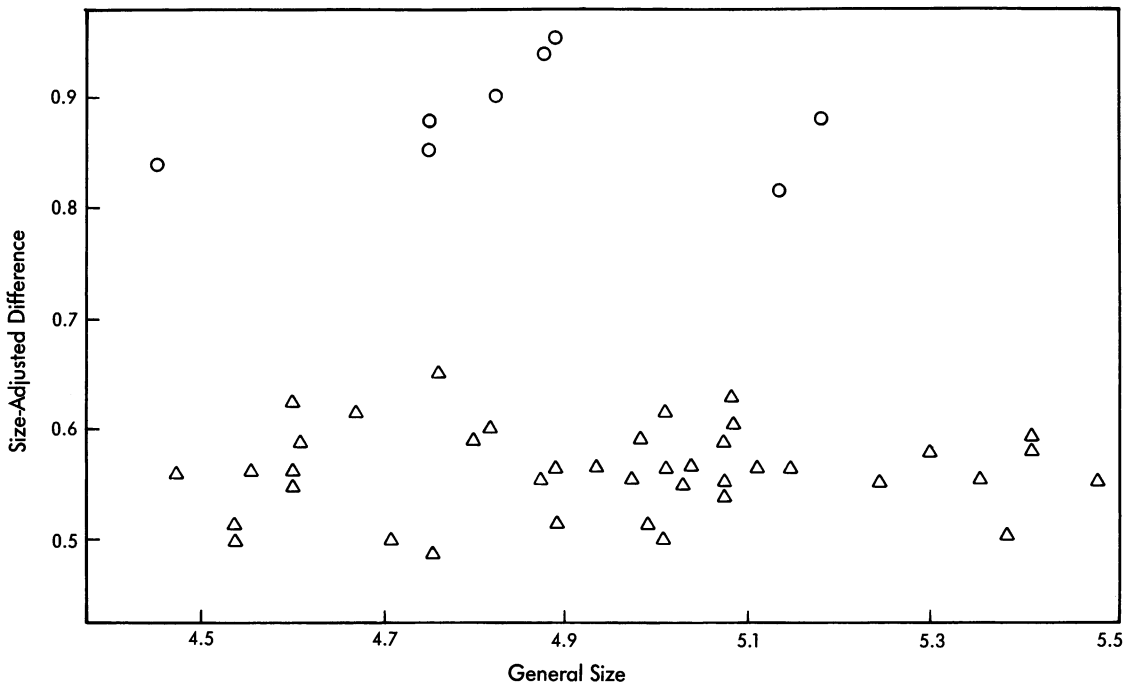


Fig. 15. Specimen scores of *Sigmodon hispidus* (open triangles, from Venezuelan locality 18) and *S. inopinatus* (open circles, from Ecuadorean locality 4) on factors representing general size and general-size-adjusted differences.

bones; broad interorbital region; long incisive foramina; broad and long palatal bridge without conspicuous longitudinal grooves; posterior palatal foramina usually enclosed by the palatine bones; derived stapedial circulation; small auditory bullae; narrow, strongly opisthodont, ungrooved upper incisors; upper molars with opposite, obtusely rounded cusps; and first mandibular molars usually with four well-developed roots.

These characters are not sufficient to distinguish *hispidus* from some of its North American congeners, which instead differ by other traits, especially karyotypes.

KARYOTYPES: Karyotypes of South American specimens of *hispidus* reported by Kiblinksky (1969) from Rancho Grande (Venezuelan locality 8) and Barinitas (Estado Barinas, Venezuela, at 84°5'N, 70°25'W) have the same diploid number ($2n = 52$) and autosomal morphology as karyotypes of putative conspecifics from North and Central America (differences in Y-chromosome morphology, however, were remarked by Zimmerman, 1970). Two hitherto unpublished specimens from Finca El Jaguar (Venezuelan locality 45) also have 52 chromosomes that

resemble those of typical *hispidus* in gross morphology. Karyotypes from Colombian populations are unknown.

COMPARISONS: Comparisons between *hispidus* and other South American species are provided in subsequent accounts.

GEOGRAPHIC VARIATION: Evidence for significant geographic patterns of morphological variation is not apparent among available samples of South American *hispidus*. Minor aspects of pelage pigmentation or fur texture distinguish a few populations, and specimens from the upper Río Magdalena valley (e.g., Valle de Suaza in table 10) have slightly larger molars and narrower palates than samples from the Caribbean coastal plains and sierras, but I have been unable to discover any well-marked regional differences worthy of subspecific recognition.

REMARKS: South American populations with the diagnostic attributes cited above are provisionally referred to *hispidus* in the absence of any characters to distinguish them unambiguously from the typical North American form. Although average differences in craniodental morphology between South American and Florida specimens are

TABLE 10

Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Sigmodon hispidus* from South America

	Colombia		Venezuela	
	Valle de Suaza ^b (24♂, 13♀)	Minca ^c (15♂, 11♀, 2 unk.)	Montalbán ^d (21♂, 19♀)	Rancho Grande ^e (7♂, 7♀)
CIL	32.4 ± 2.5 (26.2–37.3)	32.2 ± 1.8 (28.9–36.3)	32.6 ± 2.3 (28.4–37.3)	31.7 ± 1.8 (28.1–34.7)
LD	9.3 ± 1.1 (6.9–11.6)	9.4 ± 0.8 (8.1–11.0)	9.5 ± 0.9 (7.9–11.4)	9.1 ± 0.7 (7.8–10.4)
LM	6.5 ± 0.2 (6.2–6.9)	6.2 ± 0.2 (5.9–6.5)	6.3 ± 0.1 (6.0–6.7)	6.2 ± 0.2 (6.0–6.5)
BM1	2.1 ± 0.1 (2.0–2.2)	2.0 ± 0.1 (1.9–2.2)	2.0 ± 0.1 (2.0–2.2)	2.1 ± 0.1 (2.0–2.2)
LIF	7.8 ± 0.7 (5.9–9.3)	7.7 ± 0.6 (6.9–8.9)	7.8 ± 0.7 (6.5–9.2)	7.6 ± 0.6 (6.4–8.2)
BR	6.1 ± 0.4 (5.0–6.9)	5.8 ± 0.3 (5.2–6.6)	5.9 ± 0.4 (5.1–7.0)	5.8 ± 0.4 (5.1–6.3)
BPB	2.8 ± 0.4 (2.0–4.0)	3.2 ± 0.4 (2.7–4.2)	3.3 ± 0.5 (2.4–4.4)	3.2 ± 0.4 (2.4–3.9)
BZP	4.1 ± 0.4 (3.2–5.0)	4.0 ± 0.3 (3.4–4.7)	3.8 ± 0.3 (3.2–4.4)	3.9 ± 0.3 (3.4–4.3)
LIB	5.4 ± 0.3 (4.9–6.0)	5.6 ± 0.3 (5.1–6.1)	5.4 ± 0.3 (5.0–6.1)	5.3 ± 0.3 (4.9–5.6)
DI	2.0 ± 0.2 (1.5–2.2)	1.9 ± 0.2 (1.6–2.2)	1.9 ± 0.2 (1.6–2.3)	1.9 ± 0.1 (1.6–2.0)
BIT	2.7 ± 0.3 (2.1–3.3)	2.5 ± 0.2 (2.0–3.0)	2.6 ± 0.3 (2.0–3.1)	2.6 ± 0.2 (2.1–2.8)
ZB	19.7 ± 1.2 (16.6–22.0)	19.2 ± 0.9 (17.8–21.4)	19.4 ± 1.0 (17.1–21.5)	19.3 ± 1.0 (17.2–21.1)

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).

^b Colombian locality 12; all measured specimens are from sublocality Naranjal.

^c Colombian locality 14; measured specimens are from sublocalities Minca (N = 15), Onaca (5), Masinga Vieja (5), Bonda (2), and Masinga (1).

^d Venezuelan locality 18.

^e Venezuelan locality 8; measured specimens are from sublocalities El Limón and Guamita.

not wanting, none appears to be sufficient for diagnosis. Since the South American samples are morphometrically similar to typical *hispidus* (fig. 12), and because the available karyotypes from North and South America are alike, if not identical, in chromosome number and morphology, I see no reasonable taxonomic alternative to the arrangement adopted herein.

Nevertheless, the hypothesis that a reproductively continuous series of populations extends from Colombia to Nebraska will doubtless provoke future researchers to apply more sophisticated molecular and cytological methods than have hitherto been brought to bear on the problem. Such efforts should be encouraged in the expectation that *hispidus*, as currently recognized, may prove to consist of several morphologically cryptic but genetically distinct geographical units. The Central American populations, in particular, have received no revisionary attention and merit close scrutiny by any means available.

In the event that new characters are discovered that require recognition of one or more different species for the South American populations here assigned to *hispidus*, all of the species-group names listed in the synonymy above are available. Of these, *hirsutus*

merits special attention as the oldest epithet for a South American cotton rat, and as the second-oldest name in the entire genus. I have not seen the type, but Burmeister's (1854) description and Giebel's illustration (reproduced in fig. 18), were enough for Thomas (1914) to infer that *hirsutus* is a species of *Sigmodon* with ungrooved incisors, a decision with which Tate (1932) concurred as I do also. The type (from Maracaibo) is in the zoological museum of Halle (Mohr, 1941), and should be reexamined if the name is required by some future taxonomic contingency.

SPECIMENS EXAMINED: **Colombia**—*Boyacá*, Muzo (FMNH 4); *Cesar*, El Mamón (BMNH 1, MCZ 3), Pueblo Viejo (MCZ 2, including the topotype of *sanctaemartae*), San Sebastian (FMNH 24, MCZ 9, USNM 1), El Salado (USNM 6), Pueblo Bello (FMNH 2, USNM 22); *Cundinamarca*, Bogotá (AMNH 6, BMNH 3 [including the type of *bogotensis*]), 10 km E Boquerón (AMNH 1), Caparrapi (USNM 1); *Guajira*, La Concepción (MCZ 1, USNM 1), Las Marimondas (USNM 18), San Antonio (MCZ 1), Sierra Negra (USNM 1); *Huila*, Valle de Suaza (USNM 193), 17.5 km SE Villavieja (MVZ 1); *Magdalena*, Agua Dulce (FMNH 1), Bonda (AMNH 13), Cin-

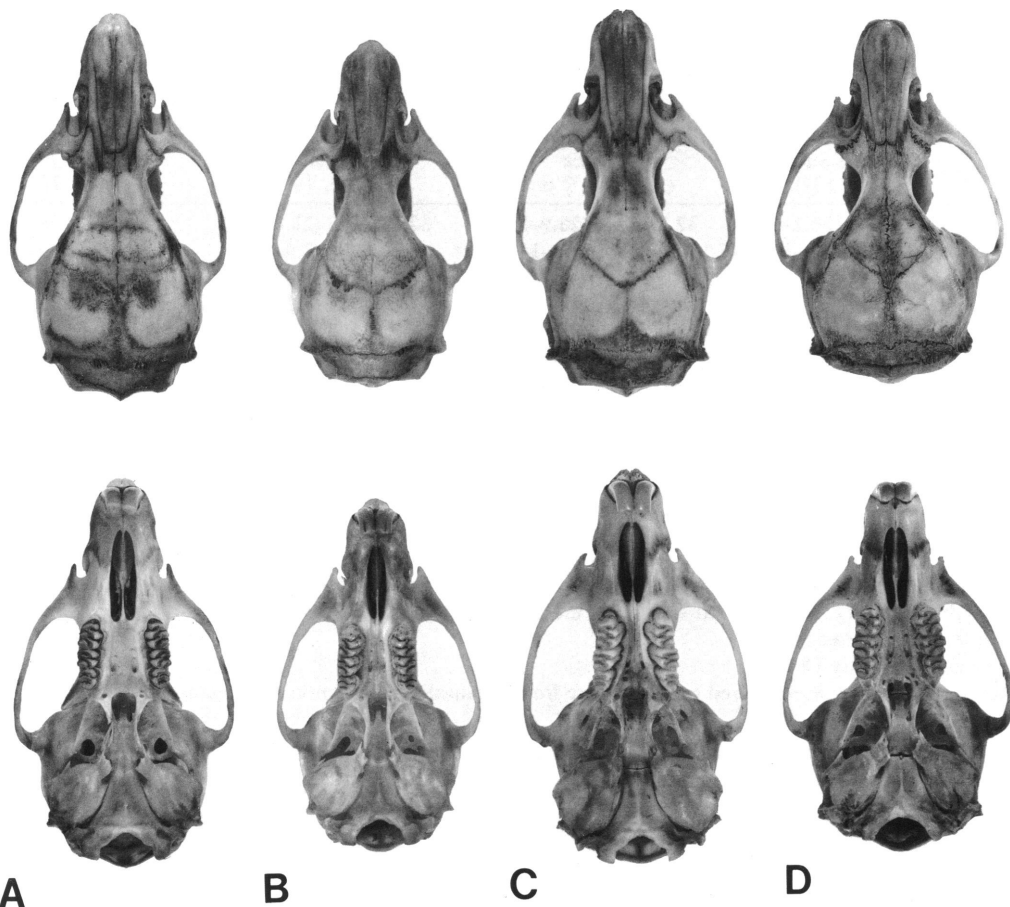


Fig. 16. Dorsal and ventral views of crania ($\times 1.5$) of South American *Sigmodon* species. A, *S. hispidus* (USNM 442531); B, *S. alstoni* (USNM 520676); C, *S. peruanus* (AMNH 67028); D, *S. inopinatus* (AMNH 66308).

cinati (FMNH 1), Mamatoca (FMNH 4), Manzanares (AMNH 3), Masinga (FMNH 3, USNM 1), Masinga Vieja (AMNH 6, USNM 1), Minca (AMNH 49, USNM 5), Onaca (AMNH 12, BMNH 4), Santa Marta (BMNH 1); *Norte de Santander*, Guamalito (USNM 5); *Santander*, Bucaramanga (MSU 9); *Tolima*, Mariquita (BMNH 4). **Venezuela**—*Aragua*, Rancho Grande (AMNH 9, UMMZ 1, USNM 29), Tiara (MHNLS 18), Camp Rangel (USNM 27); *Barinas*, Altamira (USNM 9); *Carabobo*, El Trompillo (BMNH 10), La Florida (MHNLS 2), Montalbán (USNM 66); *Cojedes*, Tucuragua (MHNLS 1), Hato Itabana (MHNLS 8), La Blanquera (MHNLS 1); *Distrito Federal*, Caracas (AMNH 3, BMNH 2, USNM 8), San Julián (USNM 1); *Falcón*, Cerro Socopo (USNM 2); *Guárico*, San Juan de los Morros (USNM 1); *Lara*,

Caserio Boro (USNM 30), San Miguel (AMNH 25); *Mérida*, Mesa Bolívar (USNM 1); *Miranda*, Curupao (USNM 1); *Yaracuy*, Finca El Jaguar (AMNH 1, MHNLS 2); *Zulia*, Novito (USNM 2). Total = 683.

Sigmodon alstoni (Thomas)
(Figures 9–11, 16, 17)

Reithrodon alstoni Thomas, 1880: 691.
Sigmomys alstoni Thomas, 1901: 150.
Sigmomys savannarum Thomas, 1901: 150.
Sigmomys venester Thomas, 1914: 412.
Sigmodon alstoni alstoni Cabrera, 1961: 508.
Sigmodon alstoni savannarum Cabrera, 1961: 508.
Sigmodon alstoni venester Cabrera, 1961: 508.

TYPE: A British Museum specimen (BMNH 47.6.23.7), consisting of the fluid-preserved carcass, skull, and mandibles of a very old

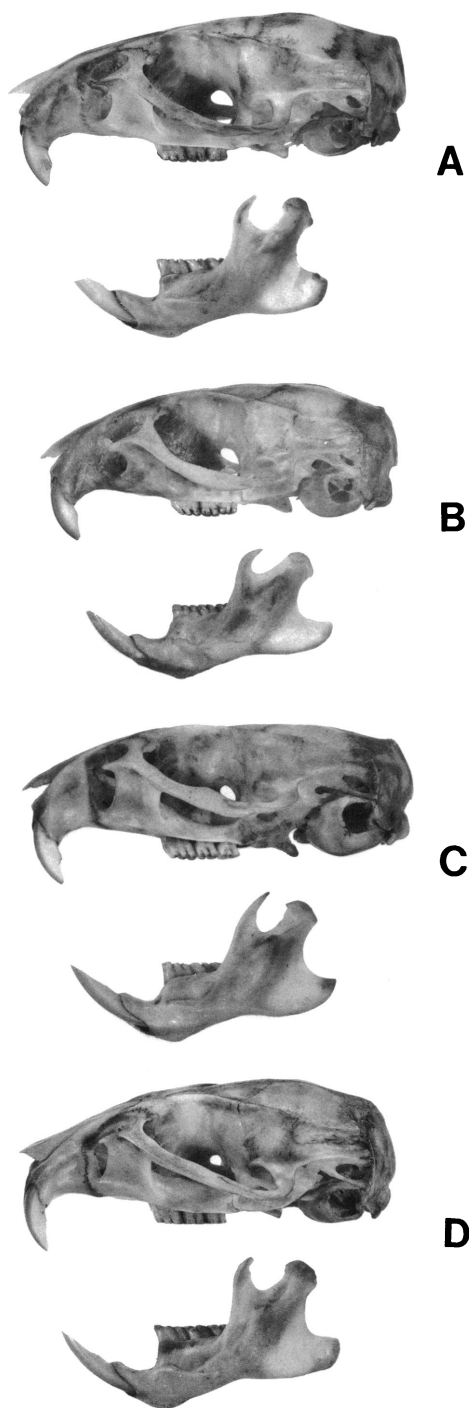


Fig. 17. Lateral views of crania ($\times 1.5$) of South American *Sigmodon* species. Species and specimens are the same as those in fig. 16.

male collected in Venezuela by D. Dyson sometime prior to 1880. The skull is missing the tip of the left nasal, both zygomatic arches, the right auditory bulla, and most of the basicranium; the heavily worn molars retain no details of occlusal morphology. Thomas (1901) restricted the type locality to Cumaná (Venezuelan locality 41).

DISTRIBUTION AND SYMPATRY: Apparently rare in the valley of the Río Cesar in extreme northeastern Colombia and in the Lake Maracaibo basin of Venezuela from which regions only a few specimens are known, but common throughout unforested and deforested habitats below about 1300 m elevation east of the Andes and south of the coastal cordilleras, including all of the Llanos,⁵ some isolated savannas in the Venezuelan state of Amazonas, deforested regions in the northeastern Venezuelan highlands, the Gran Sabana in southeastern Venezuela, the savannas of the upper Rio Branco in Brazil, the Rupununi savannas of Guyana, the coastal and interior savannas of Surinam, and contiguous savannas in the upper Rio Paru drainage of the Brazilian state of Pará. No specimens have yet been collected in French Guiana, but *alstoni* should occur in the coastal savannas there and in the neighboring Brazilian state of Amapá. The species is known from cave fossils presumed to be of late Pleistocene age from Tobago (Eshelman and Morgan, 1985) but is apparently not part of any Recent insular fauna.

Geographic overlap and sympatry between *alstoni* and *hispidus* have already been described in the account for the latter species.

MORPHOLOGICAL DIAGNOSIS: A small species of *Sigmodon* distinguishable from other congeners by its broad, strongly opisthodont, and deeply grooved upper incisors. Addi-

⁵ The distribution of *alstoni* in the Llanos of Colombia is more extensive than that suggested by the single locality plotted in fig. 1. Specimens in the collections of the Universidad del Valle (in Cali) document the presence of this species at San Juan de Arama and Puerto Gaitan (in Departamento Meta), and from the vicinity of Puerto Carreño (near the confluence of the Río Meta and the Orinoco in Comisaría Vichada) according to M. Alberico (in litt.). Groove-toothed cotton rats probably range throughout the eastern Colombian savannas, which extend from the Venezuelan border south to the Río Guaviare.

TABLE 11
Diploid Chromosome Counts of Venezuelan Specimens of *Sigmodon alstoni*

Locality	Field number	Museum number	Sex	N ^a	Diploid count ^b
Hato El Frío ^c	RSV 1197	USNM 448698	♂	19	82
Hato El Frío ^c	RSV 1198	MHNLS 7913	♀	15	78
Hato El Frío ^c	RSV 1199	MHNLS 7914	♀	10	78
Hato El Frío ^c	RSV 1210	USNM 448639	♀	10	80
Hato El Frío ^c	RSV 1211	MHNLS 7919	♂	12	78
Hato El Frío ^c	RSV 1217	USNM 448640	♂	11	80
San Ignacio Yuruaní ^d	RSV 1018	USNM 448632	♀	12	78
San Ignacio Yuruaní ^d	RSV 1062b	MHNLS 7900	♀	8	80
San Ignacio Yuruaní ^d	RSV 1234	AMNH 257341	♀	10	80
Finca Vuelta Larga ^e	RSV 1378	AMNH 257342	♀	8	82
Finca Vuelta Larga ^e	RSV 1379	MHNLS 8151	♀	12	82

^a Number of cells analyzed.

^b Modal values.

^c Venezuelan locality 6.

^d Venezuelan locality 14.

^e Venezuelan locality 43.

tionally, *alstoni* differs from other South American species by its long nasal bones; unconstricted interorbital region; incisive foramina that usually extend to or between the molar alveoli; unconstricted palatal bridge; posterior palatal foramina always bordered by both maxillary and palatine bones; derived stapedial circulation; small auditory bullae; upper molars with opposite, obtusely rounded cusps; and first mandibular molars with only three well-developed roots.

KARYOTYPES: Diploid counts of 80 to 82 chromosomes were reported for *alstoni* by Reig et al. (1990) who cited Reig (1987) as the original source of this observation. I found no reference to *Sigmodon* karyotypes in Reig (1987), but Reig (1986) reported a diploid number of 82 for *alstoni*, citing unpublished data; the geographic origin of the karyotyped specimen(s) was not stated.

Eleven specimens that my colleagues and I karyotyped in the field at three Venezuelan localities have modal counts of 78 to 82 chromosomes (table 11). The modes for most specimens are well defined and appear to be inversely correlated with the number of large metacentric (or submetacentric) elements present; Robertsonian polymorphism is a plausible explanation for this variability, but karyotypes with such high counts are difficult to analyze and this interpretation is conjectural.

A single male from Caripito (Venezuelan

locality 36) karyotyped by J. W. Bickham and M. D. Engstrom had a modal count of 80 chromosomes (Bickham, in litt.)

COMPARISONS: Hershkovitz (1955) suggested that the genus *Sigmomys* was based on specimens of South American *Sigmodon hispidus* with grooved incisors, but the conspecificity of *alstoni* and *hispidus* can be rejected unequivocally on several grounds. Firstly, the upper incisor grooves do not have the aspect of a population polymorphism: there are no intermediate morphologies, specimens from the broad geographic zone of overlap having either deep, well-defined grooves or none at all. Secondly, other morphological characters, especially measurements, are correlated with the presence of grooved incisors; this has already been demonstrated for the multivariate data (figs. 12, 13), but is also obvious from univariate comparisons (e.g., of hindfoot length in table 1; and of molar length, LM, in tables 10 and 12). The two incisor phenotypes also differ significantly in frequencies of alternative morphologies of the posterior palatal foramina (table 4) and of the lingual root of m1 (table 5). Finally, conspicuous differences in karyotypes ($2n = 52$ for smooth-toothed rats, and $2n = 78$ to 82 for groove-toothed specimens) would appear to preclude any effective genetic exchange between the two forms where they occur sympatrically.

No close comparisons are required with

TABLE 12
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Sigmodon alstoni*

	Rancho Grande ^b (17♂, 9♀)	Hato El Frio ^c (9♂, 7♀)	San Antonio Maturín ^d (4♂, 8♀)	Kanuku Mountains ^e (7♂, 7♀)
CIL	28.4 ± 1.7 (25.0–31.2)	29.8 ± 1.4 (27.2–31.4)	28.5 ± 2.1 (25.8–31.2)	28.5 ± 1.5 (25.8–30.6)
LD	8.3 ± 0.7 (6.9–9.4)	8.8 ± 0.6 (7.8–9.6)	7.9 ± 0.9 (6.8–9.2)	8.1 ± 0.6 (7.0–9.2)
LM	5.2 ± 0.2 (4.8–5.6)	5.5 ± 0.2 (5.2–5.8)	5.7 ± 0.1 (5.6–5.9)	5.4 ± 0.1 (5.2–5.6)
BM1	1.8 ± 0.1 (1.6–2.0)	2.0 ± 0.1 (1.9–2.1)	2.0 ± 0.1 (1.9–2.2)	2.0 ± 0.1 (1.9–2.1)
LIF	6.6 ± 0.5 (5.4–7.5)	7.1 ± 0.4 (6.4–7.8)	6.5 ± 0.7 (5.6–7.6)	6.7 ± 0.4 (6.0–7.2)
BR	4.9 ± 0.2 (4.2–5.4)	5.0 ± 0.4 (4.4–5.5)	4.7 ± 0.3 (4.2–5.2)	5.0 ± 0.3 (4.3–5.6)
BPB	2.6 ± 0.3 (2.2–3.2)	2.9 ± 0.4 (2.2–3.6)	2.5 ± 0.4 (2.0–3.2)	2.7 ± 0.3 (2.1–3.4)
BZP	3.3 ± 0.3 (2.5–3.9)	3.4 ± 0.3 (2.6–3.7)	3.2 ± 0.4 (2.8–3.8)	3.4 ± 0.2 (3.0–3.6)
LIB	4.6 ± 0.2 (4.0–5.0)	4.8 ± 0.1 (4.5–5.0)	4.6 ± 0.2 (4.2–5.1)	4.5 ± 0.2 (4.2–5.0)
DI	1.6 ± 0.1 (1.4–1.9)	1.8 ± 0.1 (1.4–2.0)	1.7 ± 0.2 (1.4–2.0)	1.8 ± 0.1 (1.6–1.9)
BIT	2.3 ± 0.3 (1.7–2.8)	2.6 ± 0.2 (1.9–2.8)	2.3 ± 0.3 (1.9–2.9)	2.7 ± 0.2 (2.2–3.0)
ZB	17.2 ± 0.9 (15.1–19.0)	17.8 ± 0.8 (16.2–18.7)	17.3 ± 1.0 (15.9–19.0)	17.2 ± 0.7 (16.0–18.6)

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).

^b Venezuelan locality 8; measured specimens are from sublocality El Limón.

^c Venezuelan locality 6.

^d Venezuelan locality 39.

^e Guyana locality 2; includes the type of *Sigmomys savannarum*.

peruanus and *inopinatus*, geographically remote smooth-toothed species differing from *alstoni* in many other attributes that are listed in their respective diagnoses below.

GEOGRAPHIC VARIATION: Available population samples exhibit modest variation in pelage color and texture. Lowland populations (e.g., those from the Rupununi savannas of Guyana, from the upper Río Branco drainage of Brazil, and from the lower Llanos) have short, close, coarse fur, whereas specimens collected at higher elevations (e.g., those from the Gran Sabana and the eastern Caribbean highlands of Venezuela) have softer, longer, and denser pelage. Skins from Guyana and Brazil are also paler than other specimens, a contrast that perhaps is correlated with soil color.

Some average differences in craniodental measurements among available population samples of *alstoni* are noteworthy (e.g., the contrast in molar toothrow length between Rancho Grande and San Antonio Maturín, table 12) but do not appear to represent any consistent geographic pattern. Since the magnitude of overall morphometric divergence among these samples is similar to that observed within other South American *Sigmodon* species (fig. 12), and because population differences in qualitative aspects of cranial morphology are very slight, the re-

tention of *venester* and *savannarum* as subspecies serves no purpose at the present time. Both names are available, however, should significant geographic patterns of molecular or cytological divergence be discovered in future studies.

REMARKS: Thomas (1901) erected *Sigmomys* in recognition of the many morphological characters that distinguish *alstoni* from *Reithrodon*, to which genus the species was first referred. "Altogether," he remarked, "it seems probable that this form is rather a groove-toothed *Sigmodon* than any close relation to *Reithrodon*" (op. cit.: 150). Hershkovitz (1955, 1966b) and Cabrera (1961) concluded that *alstoni* is only what Thomas suggested, a species of *Sigmodon* with grooved incisors, and treated *Sigmomys* as a subjective junior synonym. Persistent opinions to the contrary, that *Sigmomys* should be retained as a valid taxon (Husson, 1978; Williams et al., 1983), are based on the supposed "importance" of incisor grooves for muroid classification. Special recognition for favored characters, however, has no place in rational systematic practice: grooved incisors are merely an autapomorphy of the species *alstoni* and no tangible biological purpose is served by retaining a monotypic higher taxon to reflect this solitary distinction.

SPECIMENS EXAMINED: Brazil—Pará, Serra

do Tumucumaque (USNM 1); *Roraima*, Frechal (AMNH 1), Limo (AMNH 18), Serra da Lua (BMNH 14, FMNH 10, MCZ 1). **Colombia**—*Guajira*, Villanueva (USNM 1); *Meta*, Los Micos (FMNH 8). **Guyana**—*Rupununi*, Dadanawa (ROM 11), Kanuku Mountains (AMNH 2, BMNH 12 [including the type of *savannarum*]), Nappi Creek (ROM 10). **Surinam**—*Nickerie*, Sipaliwini-savanne-vliegeveld (RMNH 2); *Para*, Zanderij (RMNH 2). **Venezuela**—no other data (BMNH 1, the type of *alstoni*); *Amazonas*, Paria Grande (USNM 2), Rueda (USNM 2), San Juan Manapiare (MHNLS 3, USNM 4); *Anzoátegui*, Río Oritupano (MHNLS 1); *Apure*, Entrada La Yaguita (MHNLS 1), Hato Cariben (USNM 2), Hato El Frío (AMNH 4, MHNLS 15, USNM 8), 41 km NW Puerto Páez (USNM 7); *Aragua*, Rancho Grande (USNM 28), Camp Rangel (USNM 1); *Bolívar*, El Llagual (AMNH 1), Hato La Florida (USNM 4), Mount Roraima (AMNH 19), San Ignacio Yuruaní (AMNH 1, MHNLS 1, USNM 2), Vetania (USNM 3); *Carabobo*, El Trompillo (BMNH 1, the type of *venester*); *Cojedes*, Hato El Tirado (MHNLS 2), Hato Itabana (MHNLS 8), Hato Los Caballos (MHNLS 1); *Guárico*, Calabozo (USNM 1), Hato La Merreña (MHNLS 3), Parcela 200 (MHNLS 12); *Monagas*, Caripe (USNM 4), Caripito (AMNH 1, TCWC 1), Cocollar (AMNH 5, BMNH 1), Hato Mata de Bejuco (USNM 16), San Antonio Maturín (AMNH 23), Campo Alegre (BMNH 1); *Portuguesa*, Los Mamonés (USNM 1); *Sucre*, 40 km NW Caripito (TCWC 1), Cumaná (USNM 5), Cumanaoa (AMNH 13), Finca Vuelta Larga (AMNH 1, MHNLS 2), Manacal (USNM 5); *Zulia*, Empalado Savannas (FMNH 3), Río Aurare (FMNH 4), Río Cogollo (FMNH 7, MCZ 1). Total = 326.

Sigmodon peruanus J. A. Allen
(Figures 6–8, 10, 11, 16, 17)

- Sigmodon peruanus* J. A. Allen, 1897a: 118.
Sigmodon simonsi J. A. Allen 1901: 40.
Sigmodon puna J. A. Allen, 1903: 99.
Sigmodon chonensis J. A. Allen, 1913: 479.
Sigmodon lonnbergi Thomas, 1921: 448.
Sigmodon hispidus chonensis Cabrera, 1961: 508.
Sigmodon hispidus peruanus Cabrera, 1961: 509.
Sigmodon hispidus puna Cabrera, 1961: 509.
Sigmodon hispidus simonsi Cabrera, 1961: 509.

- Sigmodon peruanus peruanus* Reig, 1986: 407.
Sigmodon peruanus simonsi Reig, 1986: 407.
Sigmodon peruanus chonensis Reig, 1986: 407.
Sigmodon peruanus puna Reig, 1986: 407.

TYPE: A specimen in the American Museum of Natural History consisting of the separately cataloged skin (AMNH 11818) and skull with mandibles (AMNH 10110) of an old adult female collected by O. T. Baron on 25 May 1895 at Trujillo, Departamento La Libertad, Peru. The skin is intact and undamaged but the skull lacks both auditory bullae, the basioccipital, and much of the lateral wall of the braincase below the squamosal root of the left zygomatic arch; the pterygoid region is largely destroyed as well, and the angles of both mandibles are broken. The molar dentition is worn almost to the roots and retains only traces of the occlusal pattern.

DISTRIBUTION AND SYMPATRY: In xeric, semiarid, and deforested landscapes of the Pacific coastal plain and adjoining Andean foothills below about 1600 m elevation in western Ecuador and northwestern Peru. The known range extends in latitude from about 8°S almost to the equator.

Sigmodon peruanus is not known to be sympatric with any congeneric species.

MORPHOLOGICAL DIAGNOSIS: A large species of *Sigmodon* distinguished from all other congeners by its complete, primitive stapedial circulation. From other South American species, *peruanus* can also be distinguished by its long nasal bones; unconstricted interorbital region; short incisive foramina (seldom extending to or between the molar alveoli); very narrow, short, and grooved palatal bridge with deep posterolateral sulci; posterior palatal foramina always bordered by both maxillary and palatine bones; large auditory bullae; broad, strongly opisthodont, ungrooved upper incisors; upper molars with alternate, acutely angled cusps; and first mandibular molars usually with only three well-developed roots.

KARYOTYPES: Unknown.

COMPARISONS: Considered conspecific with *hispidus* by Cabrera (1961), *peruanus* nevertheless differs from that taxon in many respects. In addition to possessing a pattern of stapedial arterial supply unique in the genus, *peruanus* can be distinguished from *hispidus*

TABLE 13
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Sigmodon peruanus*

	Isla Puná ^b (17♂, 16♀, 1 unk.)	Chongoncito ^c (10♂, 6♀)	Puente de Chimbo ^d (7♂, 5♀)
CIL	31.8 ± 1.5 (28.5–35.2)	31.4 ± 1.9 (28.7–34.2)	30.9 ± 1.5 (28.3–33.2)
LD	8.7 ± 0.6 (7.6–9.9)	8.8 ± 0.8 (7.5–10.0)	8.8 ± 0.7 (7.6–10.1)
LM	7.0 ± 0.2 (6.6–7.3)	6.8 ± 0.3 (6.3–7.2)	6.7 ± 0.2 (6.3–7.0)
BM1	2.2 ± 0.1 (2.0–2.3)	2.1 ± 0.1 (2.0–2.3)	2.1 ± 0.1 (2.0–2.2)
LIF	6.3 ± 0.5 (5.3–7.3)	6.4 ± 0.7 (5.4–7.6)	6.6 ± 0.5 (5.7–7.4)
BR	5.7 ± 0.3 (5.3–6.7)	5.7 ± 0.4 (5.1–6.4)	5.6 ± 0.3 (5.1–6.1)
BPB	2.2 ± 0.2 (1.9–2.9)	2.2 ± 0.3 (1.7–2.8)	2.5 ± 0.4 (1.9–3.0)
BZP	3.9 ± 0.4 (3.2–4.5)	3.9 ± 0.3 (3.5–4.4)	4.0 ± 0.3 (3.5–4.5)
LIB	5.0 ± 0.2 (4.6–5.6)	5.0 ± 0.3 (4.5–5.4)	5.0 ± 0.3 (4.6–5.4)
DI	1.9 ± 0.1 (1.7–2.2)	1.8 ± 0.1 (1.6–2.0)	1.9 ± 0.1 (1.6–2.0)
BIT	2.7 ± 0.2 (2.3–3.2)	2.7 ± 0.2 (2.3–3.0)	2.9 ± 0.1 (2.7–3.2)
ZB	18.9 ± 0.8 (16.6–20.5)	18.5 ± 1.0 (17.2–20.4)	18.4 ± 0.6 (17.1–19.4)

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).

^b Ecuadorean locality 13; measured specimens are from both sublocalities.

^c Ecuadorean locality 11.

^d Ecuadorean locality 3.

by craniodental proportions that include shorter incisive foramina, a conspicuously narrower and shorter palate, broader zygomatic plates, larger auditory bullae, and broader incisors; these contrasts are represented in the morphometric analyses described earlier (except for palatal length and bullar size, which were not measured), and can be confirmed visually from cranial photographs (figs. 16, 17). Also, the unworn upper molars of *peruanus* have alternating, sharp-angled cusps, whereas those of *hispidus* and other *Sigmodon* species have opposite, obtusely rounded cusps. Other comparisons involve qualitative trait frequencies that are less satisfactory for diagnosis but which nonetheless document substantial differences. The posterior palatal foramina of *hispidus* are usually contained only by the palatine bones, but those of *peruanus* are always bordered both by maxillaries and palatines (table 4). Also, the first maxillary molars of *peruanus* usually have only three well-developed roots, by contrast with the four well-developed roots that usually anchor this tooth in *hispidus* (table 5).

From geographically adjacent populations of *inopinatus*, *peruanus* is easily distinguished by its longer nasal bones, much broader interorbital region, shorter incisive foramina, narrower palate, primitive stapedial circulation (versus derived), larger au-

ditory bullae, more strongly opisthodont upper incisors, and first maxillary molars usually with three (versus four) well-developed roots.

GEOGRAPHIC VARIATION: Skins from the island of Puná and from northwestern Peru are paler than most specimens from the Ecuadorean mainland, but there is no evidence that this color variation is anything more than concealing pigmentation that may be expected to vary clinally with local soils. None of the cranial dimensions cited by Allen (1901, 1903, 1913) and Thomas (1921) in their descriptions of nominal species here synonymized with *peruanus* exceed the normal range of individual and ontogenetic variation within such large samples as those from Chongoncito, Puente de Chimbo, and Isla Puná (table 13). Close study of the available material suggests that, with the exception of pelage color, this is a phenotypically homogeneous species with no natural subdivisions worthy of trinomial recognition.

SPECIMENS EXAMINED: **Ecuador**—Azuay, Tunguilla Valley (FMNH 6); Chimborazo, Puente de Chimbo (AMNH 40); El Oro, Piedras (FMNH 1), Portovelo (AMNH 1), Santa Rosa (AMNH 5, BMNH 1); Guayas, Balzar Mountains (BMNH 1), Bucay (AMNH 4), Cerro Manglaralto (AMNH 6), Hacienda El Refugio (USNM 1), Chongón (BMNH 1), Chongoncito (AMNH 48), Guayaquil (AMNH 3, BMNH 1, USNM 1), Durán

(AMNH 5), G and Q RR kilometer 8 (AMNH 4), Puná (AMNH 11, BMNH 6 [including the type of *puna*]), San Ramón (AMNH 24), Pacaritambo (MNHN 1); *Loja*, Casanga Valley (AMNH 7), Malacatos (FMNH 1), Pindal (USNM 1); *Los Ríos*, Limón (AMNH 6), Quevedo (BMNH 1 [the type of *lonnbergi*]), Río Babahoyo (MNHN 6), San Carlos (MSU 2), Vinces (AMNH 13, USNM 2); *Manabí*, Chone (AMNH 10 [including the type of *chonensis*]), Río de Oro (AMNH 1). **Peru**—*La Libertad*, Pacasmayo (FMNH 3), Trujillo (AMNH 1 [the type of *peruanus*], USNM 4); *Lambayeque*, Eten (AMNH 3, BMNH 2 [including the type of *simonsi*]); *Piura*, El Arenal (USNM 2), Huásimo (FMNH 1), Jilili (MCZ 1), Lancones (USNM 1); *Tumbes*, El Sauce (USNM 3), Matapalo (FMNH 1), Positos (FMNH 5), Tumbes (USNM 1). Total = 248.

Sigmodon inopinatus Anthony

(Figures 6, 10, 11, 16, 17)

Sigmodon inopinatus Anthony, 1924: 3.

Sigmodon hispidus inopinatus Cabrera, 1961: 509.

TYPE: A specimen in the American Museum of Natural History (AMNH 66310) consisting of the skin, skull, and mandibles of an adult female collected by G. H. H. Tate on 26 October 1923 at Urbina, Provincia Chimborazo, Ecuador. The skin and skeletal materials are undamaged.

DISTRIBUTION AND SYMPATRY: Known from only two localities at high elevations in the Ecuadorean Andes. The type series was collected at 11,400 ft (3508 m) near Chimborazo in the province of that name, and several additional examples have recently been collected between 3750 and 3800 m near Cuenca in Provincia Azuay.

Sigmodon inopinatus is not known to be sympatric with any congeneric species.

MORPHOLOGICAL DIAGNOSIS: A large species of *Sigmodon* distinguished from other congeners by its short nasal bones (exposing the incisors to dorsal view); very narrow interorbital region; long incisive foramina (usually, but not always extending between the molar alveoli); unconstricted palatal bridge; posterior palatal foramina usually bordered both by maxillaries and palatines; derived stapedial circulation; small auditory bullae; procumbent (but still weakly opisthodont),

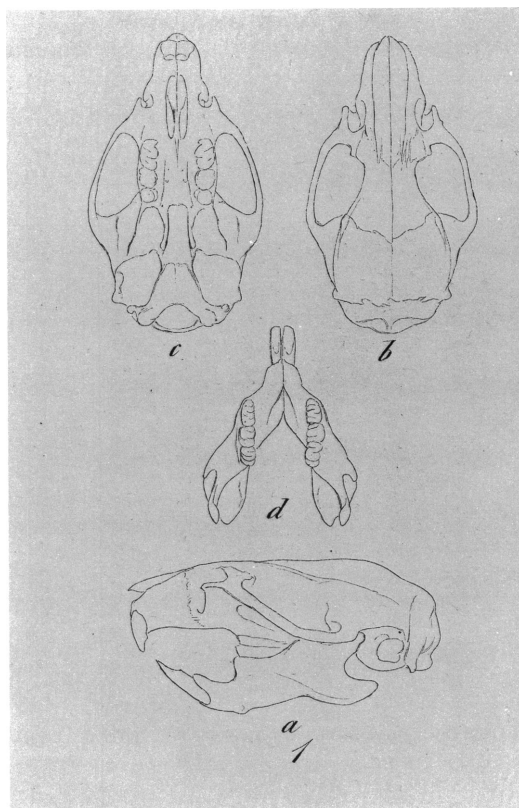


Fig. 18. Figure 1 from plate V of Giebel (1857), illustrating the skull and mandibles of "*Lasiuromys*" *hirsutus* (= *Lasiomys hirsutus* Burmeister).

ungrooved upper incisors; upper molars with opposite, obtusely rounded cusps; and first mandibular molars usually with four well-developed roots.

KARYOTYPES: Unknown.

COMPARISONS: *Sigmodon inopinatus* differs from *hispidus* by its shorter nasals, very constricted (versus broad) interorbital region, narrower and shorter palate, posterior palatal foramina usually bordered by both maxillary and palatine bones (versus usually enclosed in the palatines), and broader, more procumbent incisors.

Comparisons with the geographically adjacent species *peruanus* were provided in the preceding account.

GEOGRAPHIC VARIATION: The material available from Las Cajas conforms closely with the type series in measurements and qualitative characters. The only discrepancy worthy of note is the interorbital measurement (LIB) of the single adult Las Cajas skull,

TABLE 14
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Sigmodon inopinatus*

	Urbina ^b (28, 69)	Las Cajas ^c (BMNH 82.814 ♂)
CIL	32.6 (29.4–34.8)	34.2
LD	9.5 (8.0–10.6)	10.5
LM	6.7 (6.6–6.8)	6.8
BM1	2.2 (2.1–2.4)	2.2
LIF	7.3 (6.4–8.1)	7.8
BR	6.0 (5.5–6.5)	6.6
BPB	2.7 (2.3–3.4)	3.0
BZP	4.0 (3.4–4.6)	3.9
LIB	4.3 (4.0–4.4)	4.8
DI	1.9 (1.6–2.0)	2.0
BIT	2.8 (2.3–3.1)	3.3
ZB	20.2 (18.7–21.4)	21.6

^a The mean and the observed range only are provided for the Urbina sample; too few specimens are available to provide a meaningful estimate of the standard deviation.

^b Ecuadorean locality 4.

^c Ecuadorean locality 1.

which somewhat exceeds the range of variation among the Urbina specimens (table 14).

SPECIMENS EXAMINED: Ecuador—Azuay, Las Cajas National Park (BMNH 4); Chimborazo, Urbina (AMNH 12, including the type). Total = 16.

NATURAL HISTORY

South American species of *Sigmodon* have not been the subjects of any comprehensive natural history studies, and such information as exists must be gleaned from a few papers on special ecological topics, some general faunal reports that include sparse observations on habitats, and the unpublished fieldnotes of collectors. The latter, quoted or abstracted below, are preserved in the archives of the Department of Mammalogy at the American Museum of Natural History and the Division of Mammals at the Field Museum of Natural History.

SPECIES DESCRIPTIONS

***Sigmodon hispidus*:** Despite abundant South American material of this species in museums, the only series accompanied by

ecological information are those collected by the Smithsonian Venezuelan Project from 1965 to 1968; Handley (1976: 53) summarized data from 326 specimens:

Found . . . near streams, irrigation ditches, and other moist areas (91 percent) and only rarely in dry sites (9 percent); usually in grass, but rarely in weeds, bushes, and houses; in croplands (44 percent), savannas and pastures (31 percent), yards and orchards (16 percent), and in grassy openings in forest (9 percent).

Noteworthy in this laconic synopsis, as in numerous ecological descriptions of North and Central American populations (e.g., Aldrich and Bole, 1937; Bailey, 1905; Goertz, 1964; Goertz and Long, 1973; Goldman, 1920; Kaufman and Fleharty, 1974; Odum, 1955), is an affinity for natural or anthropogenic nonforest habitats that are usually dominated by grass. All South American collection localities for this species are either in regions where nonforest vegetation predominates for edaphic or climatic reasons (such as the northwestern Llanos, and the semiarid upper Río Magdalena valley; see Voss, 1991) or regions where extensive deforestation has accompanied human settlements; no specimens are known to have been collected in undisturbed rain forest. Fifty South American collection localities range in elevation from near sea level to about 2600 m, but *hispidus* is most often taken between 500 and 1500 m (fig. 19).

At El Limón and Guamita (both near Venezuelan locality 8), C. O. Handley, Jr. and D. I. Rhyme collected *hispidus* and *alstoni* together, in traplines set in fallow agricultural fields; no microhabitat differences were apparent from their field observations (Handley, personal commun.). Elsewhere, the circumstances of sympatry remain undescribed, and future collectors should be alert to ecological nuances that might distinguish the two species where they occur together.

All of the 326 specimens of *hispidus* obtained by the Smithsonian Venezuelan project (Handley, 1976) were taken on the ground, as were three specimens that I collected at Finca El Jaguar (Venezuelan locality 45). In North and Central American habitats the species may be active both in the daytime and at night (Aldrich and Bole, 1937; Cameron et al., 1979; Harper, 1927; Hoffmeister,

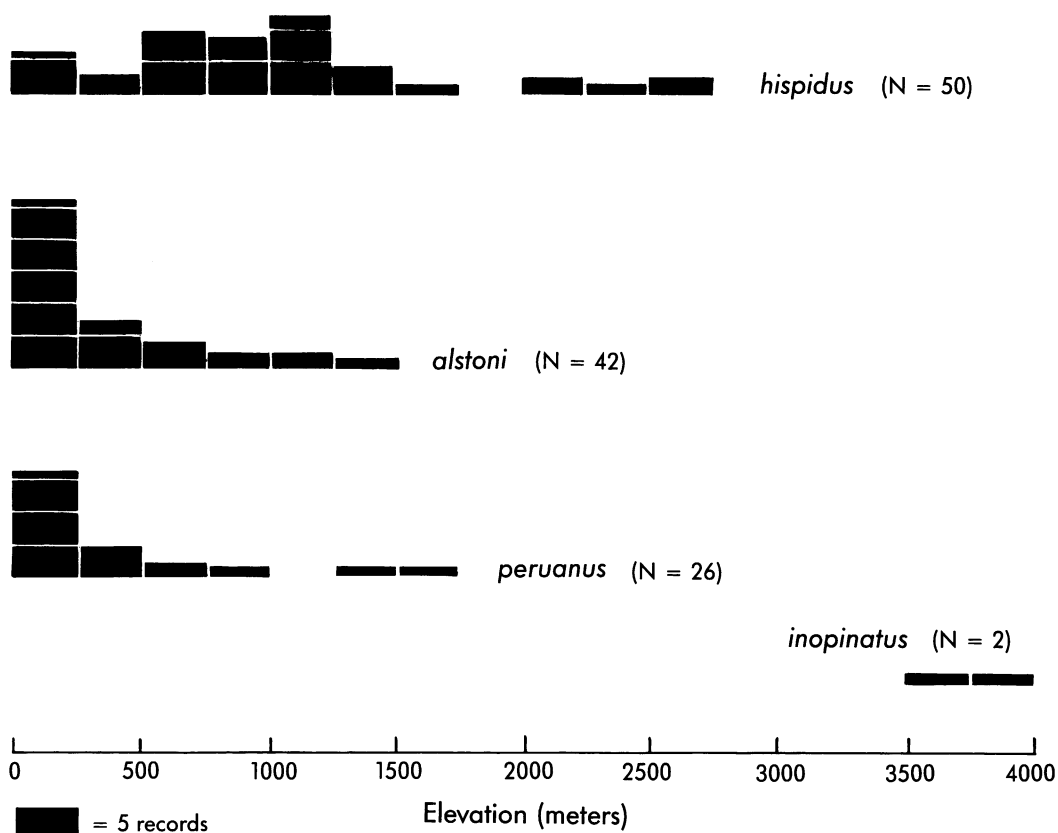


Fig. 19. Frequency histograms of elevation records for South American species of *Sigmodon*.

1986; Lowery, 1974), and is said to construct runways (Aldrich and Bole, 1937; Bailey, 1905; Goldman, 1920; Harper, 1927), but no published observations are available to confirm these behavioral traits for South American populations. The diet of *hispidus* in the Llanos consists principally of the green parts of grasses and herbaceous dicots (Vivas and Calero, 1988), a result consistent with dietary analyses of North American populations (e.g., Fleharty and Olson, 1969; Kincaid and Cameron, 1982).

Information from a few field studies of demography and reproduction in Venezuela was summarized by Vivas and Calero (1985, 1988): reproductive activity in local populations of *hispidus* is apparently continuous throughout the annual cycle of flooding and drought that characterizes the lower Llanos, but may be most intense in the rainy season when population densities also seem highest.

In South America, remains of *Sigmodon*

hispidus have been recovered from the stomachs of the fox *Cerdocyon thous* and the ocelot *Felis pardalis* (Bisbal, 1986; Bisbal and Ojasti, 1980), but the species is probably important in the diets of many other sympatric vertebrate carnivores.

Arthropod ectoparasites of *Sigmodon hispidus* collected by the Smithsonian Venezuelan Project (Handley, 1976) were described by Furman (1972), Jones et al. (1972), Johnson (1972), Tipton and Machado-Allison (1972), Brennan and Reed (1975), and Saunders (1975).

***Sigmodon alstoni*:** The groove-toothed cotton rat is usually encountered in open, grassy habitats; examples typically cited in the literature include savannas, airfields, pastures, overgrown garden plots, and weedy roadsides (Handley, 1976; Husson, 1978; Ibáñez and Moreno, 1982; O'Connell, 1981; Osgood, 1912; Tate, 1939; Vivas, 1986; Williams et al., 1983). Descriptions of two localities where



Fig. 20. The lower Llanos near Hato El Frío (Venezuelan locality 6). During the wet season (when this photograph was taken) *Sigmodon alstoni* inhabits unflooded grassy *bancos* and the weedy margins of *matas* (islands of low forest in the background); during the dry season, however, *S. alstoni* occurs throughout the savanna. Photographed in September 1987.

my colleagues and I collected *alstoni* in Venezuela serve to illustrate the diversity of natural environments that the species occupies.

HATO EL FRÍO: This large cattle ranch at 60 m elevation near the Río Apure (fig. 1, Venezuelan locality 6) is representative of much of the lower Llanos in climate and vegetation. The annual average temperature is 27°C and virtually all of the total annual precipitation (probably about 1500 mm on average) occurs from April to November; in the dry season, December through March, there is scarcely any rainfall (see Voss, 1991, for references). The landscape consists of seasonally inundated savannas (fig. 20) dissected by rivers and streams with wooded banks and scattered with islands of *mata* vegetation (a semi-deciduous woodland of low stature) growing on slightly elevated soils. Most of the savanna is flooded during the rainy season, when only the *matas* and raised, grassy ridges known as *bancos* provide natural refugia for nonaquatic organisms. We collected 17 specimens of *Sigmodon alstoni* on two brief visits to Hato El Frío, from 2–8 August 1986 and from 3–7 September 1987. All were taken on the ground, along runways

under dense grass, in unflooded parts of the savanna. Another muroid species, *Zygodontomys brevicauda*, used the same runways and was always caught in greater numbers [abstracted from my fieldnotes; also see Voss, 1991, for references and a more detailed site description].

SAN IGNACIO YURUANÍ: The town of San Ignacio Yuruaní (fig. 1, Venezuelan locality 14) is situated at 850 m elevation in the Gran Sabana, a rolling landscape of savannas and forests drained by the upper Río Caroní (fig. 21). The average annual precipitation at San Ignacio is about 2100–2200 mm with some monthly variation but no extremely dry season; the average annual temperature is 21–23°C. The town was our base camp from 9–27 June 1986 and from 20 June to 7 July 1987, during which time we collected only six specimens of *Sigmodon alstoni*. All were trapped on the ground in dense grass, either in open savanna or in *arbustales*, extensive thickets of mixed evergreen shrubs and small trees interspersed with grassy openings. Two other muroid species, *Akodon* cf. *urichi* and *Zygodontomys brevicauda*, occurred syntopically with *S. alstoni* and were captured much more frequently: the former in both savanna and ar-



Fig. 21. The Gran Sabana near San Ignacio Yuruaní (Venezuelan locality 14). Open savannas dominated by the grass *Trachypogon plumosus* and scattered groves of moriche palms (*Mauritia flexuosa*) are characteristic of the region, as are the numerous low termite mounds in the background. Here *Sigmodon alstoni* was collected in meadows of dense grass in valley bottoms with rich organic soils, and in grassy openings in thickets of evergreen shrubs. Photographed in June 1986.

bustales, the latter only in *arbustales* [abstracted from my fieldnotes; also see Voss, 1991, for references and more detailed habitat accounts].

Sigmodon alstoni is a lowland species with a known elevational range from sea level to only 1300 m (fig. 19). Tate (1939) remarked that *alstoni* was found in savannas at the base of Mt. Roraima but not on the upper slopes where grasslands extend to at least 1600 m.

All of the 140 specimens of *alstoni* obtained by the Smithsonian Venezuelan project (Handley, 1976) were collected on the ground. Strictly terrestrial habits are also suggested by my field observations at the localities described above, by O'Connell's (1981) trapping results, and by the absence of any reference to other substrates in the literature cited earlier. Groove-toothed cotton rats are active in broad daylight as well as nocturnally (Ibáñez, 1980; O'Connell, 1981; Osgood,

1912; Tate, 1939; Vivas et al., 1986) and are said to construct runways (Tate, 1939; O'Connell, 1982). Ibáñez and Moreno (1982) concluded that this species is "típicamente herbívora" based on their examination of stomach contents, and captives offered a variety of foods collected from natural habitats exhibit a strong preference for grass (O'Connell, 1981).

Autopsies of 156 specimens kill-trapped in the lower Llanos of Estado Apure, Venezuela, documented pregnancies throughout the annual cycle of flooding and drought that characterizes this extremely seasonal environment, but reproductive activity may be least in the dry season; the number of embryos counted in utero ranged from two to eight, with a mean of 4.4 (Ibáñez and Moreno, 1982). The demographic studies of O'Connell (1981) and Vivas (1986) did not include reproductive autopsies, but their data also

suggest continuous reproductive activity in Llanoan populations.

Remains of *Sigmodon alstoni* have been recovered from the stomachs or scats of several mammalian carnivores including foxes (*Cerdocyon thous*), ocelots (*Felis pardalis*), jaguarundis (*Felis yagouaroundi*), and grisons (*Galictis vittata*) (Bisbal, 1986; Bisbal and Ojasti, 1980; Sunquist et al., 1989). White-tailed kites (*Elanus leucurus*) eat groove-toothed cotton rats (Husson, 1978) and most other large savanna raptors are probably important predators as well.

Arthropod ectoparasites of *Sigmodon alstoni* collected by the Smithsonian Venezuelan Project (Handley, 1976) were described by Furman (1972), Jones et al. (1972), Johnson (1972), Tipton and Machado-Allison (1972), Brennan and Reed (1975), and Saunders (1975).

***Sigmodon peruanus*:** There are no published accounts of the environments occupied by this species in western Ecuador and northwestern Peru, and the following descriptions are therefore abstracted verbatim from the manuscript journals in which G. H. H. Tate and other collectors working for the American Museum of Natural History recorded their field observations.

Tate and H. E. Wickenheiser collected 40 specimens of *Sigmodon peruanus* at Puente de Chimbo (Ecuadorean locality 3) between 3 August and 26 September 1922. Camped beside the Río Chimbo at 1134 ft (348 m) elevation, the collectors encountered a diversity of natural and manmade habitats:

There are several distinct types of collecting country here. . . . First, near the house is second-growth land and portrero [pastures]. Next, the loma [a vegetation formation peculiar to the region], forested, moderately open and dry, quite flat. Thirdly, the playas [river beaches or floodplains] and riversides, and lastly the very dense, wet montaña [forest] across the bridge from the hacienda. . . . From a collector's point of view this place is excellent, since besides this variety of country close by, the fauna is rich and varied [Tate's notes for 12 August].

The weather is generally true to the following program. At noon a light shower, clear p.m. and sunset; early in the evening the garúa [a dense nocturnal fog] sets in, often continuing until 8 o'clock the next morning. Morning fair till mid-day shower. In spite of this garúa, the whole second growth is arid. . . . The two commonest rats, *Oryzomys [talamancae]* and *Melan-*

omys [caliginosus], are quite generally distributed. *Sigmodon [peruanus]* on the other hand, I have only found in the second-growth land close to the hacienda, and in the younger part of the platanal [a garden plot] across the river, i.e., that part recently cleared, in which the logs have not decomposed [Tate's notes for 29 August].

At another camp on the 1922 expedition, near Chongoncito (Ecuadorean locality 11), Tate and Wickenheiser collected 48 specimens of *peruanus* between 8 and 12 October:

We are actually about one half hour east of Chongoncito, encamped on an "estero" [a tidal estuary]. It is only salt for a short way above camp. . . . It gets very hot [here] through the noon hours, and is of course intensely dry. The country is practically flat "Ceiba country"—thick brush interspersed with great Ceibas [Tate's notes for 6 October].

It [the landscape] is intensely dry now, but shows evidence of being the very opposite during the rains. It is not in the least comparable with [the] Santa Elena [peninsula]. That place was purely desert, not even producing cactus. . . . One thing I fail to understand is that all this part is scrub forest averaging 15–20 feet high. Now, the people state that they take excellent crops out year after year; therefore, this smallness of the trees cannot be due to poverty of soil. The apparent reason is the long and intensely dry summer season. . . . [Tate's notes for 11 October].

From 22 October to 5 November, Tate and Wickenheiser were based at Hacienda Pijigal near Vinces (Ecuadorean locality 22), where they collected 13 specimens of *peruanus*. The camp at Pijigal was located in

. . . slightly rolling [country]. . . broken here and there by very small watercourses running NE and now dry. . . vegetation scanty, [with] scattered Ceibas and, in the ravines, other trees. Nearing the river this country is at first interspersed with, and eventually gives way almost entirely to, manglars [mangroves], now dry, but in the rains anything from 6–12 feet under water [Tate's notes for 26 October].

The specimens of *peruanus* collected near Hacienda Pijigal were trapped under dense grass along the dry watercourses mentioned in the passage quoted above.

On the next American Museum expedition to Ecuador, Tate visited Hacienda San Ramón on Isla Puná (Ecuadorean locality 13), where 24 specimens of *peruanus* were collected between 23 and 28 December 1923. Tate's notes for 22 December include the observation that the arid habitats on Isla Puná

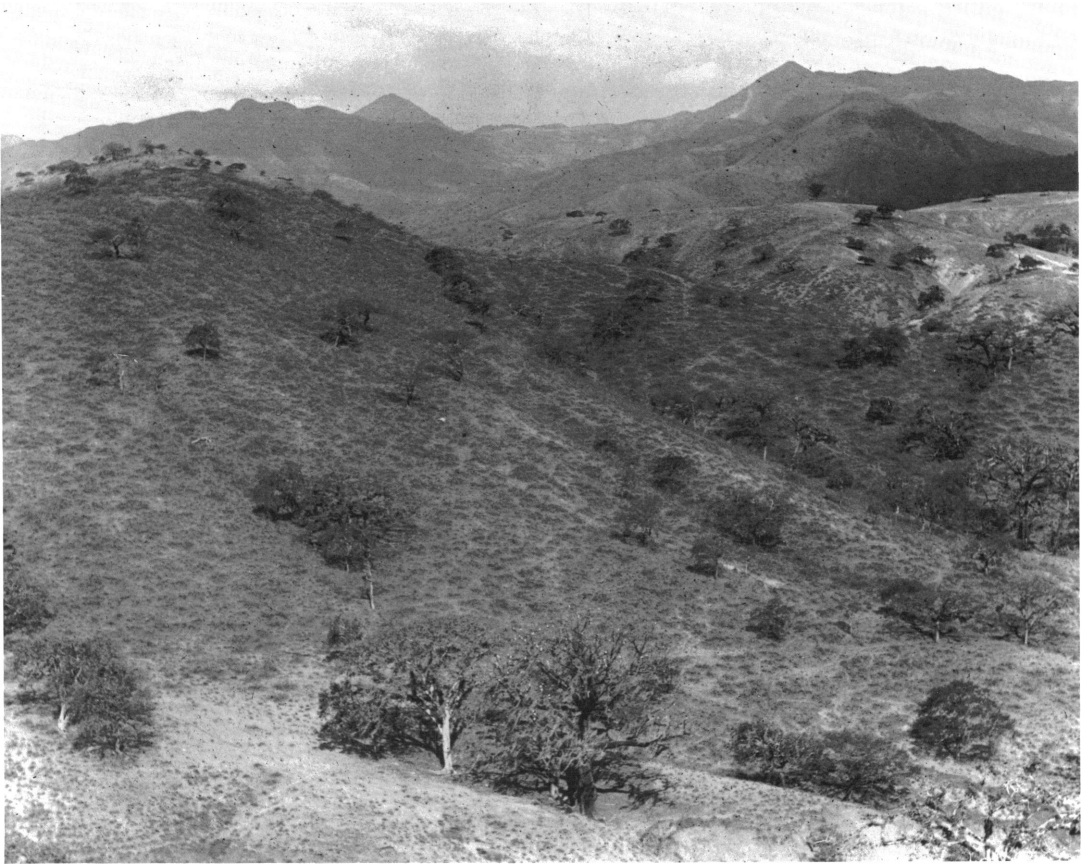


Fig. 22. Semiarid hillsides with green ceiba trees (one is in the middle foreground) in the valley of the Río Casanga (Ecuadorean locality 15). Owl pellets containing skull fragments of *Sigmodon peruanus* were collected at this locality by H. E. Anthony and G. K. Cherrie. Photographed in September 1920 by H. E. Anthony.

appeared almost identical with those described above at Chongoncito.

The only photographs suitable for reproduction of landscapes inhabited by *peruanus* (figs. 22, 23) were taken by H. E. Anthony in September 1920 when he camped in the valley of the Río Casanga (Ecuadorean locality 15) with G. K. Cherrie. There they only collected owl pellets containing fragments of seven cotton rat skulls, but Anthony's vivid rendition of the setting is consistent with Tate's prosaic but more analytical descriptions of *peruanus* habitats elsewhere:

The Casanga valley is an open, extremely arid and desolate ravine, everywhere fearfully eroded . . . Although a desert for most of the year, evidently the rains when they do come are exceedingly heavy. Great stretches of the floor and slopes of this valley are either barren or else sparsely clothed with thorny mesquite

or cactus. A beautiful grove of green-barked Ceibas extending some four or five miles down the valley in scattered groups is the one redeeming floral feature. . . The only spots where rodents can exist is where fields are fenced to keep the goats out.

A feature apparently common to all of the habitats in which *peruanus* was collected by AMNH expeditions in western Ecuador is the dramatic seasonality of rainfall. The local rainy "winter" or *invierno* ends in April or May, and the dry "summer" or *verano* lasts from June to October or even December (Johnson, 1976). Between 100 and 800 m elevation, condensation from nocturnal fog (the *garúa*; see Tate's account for Puente de Chimbo, above; and Chapman, 1926: 706–707) provides sufficient moisture during the seasonal drought to support a perennially green *loma* vegetation, but elsewhere in the



Fig. 23. Green ceibas (*Ceiba* sp., Bombacaceae), characteristic and conspicuous trees with bright greenish bark in the semiarid habitats where *Sigmodon peruanus* is abundant in western Ecuador. Photographed in the valley of the Río Casanga (Ecuadorean locality 15) by H. E. Anthony in September 1920.

Ecuadorean coastal lowlands south of Manta, deciduous woodlands, thornscrub, and dry grasslands predominate. On the Santa Elena

peninsula, and in coastal Peru, these semiarid formations are replaced by real deserts. Within this climatic region, *peruanus* appears re-



Fig. 24. *Páramo* grasslands on the eastern slopes of Chimborazo above Urbina (Ecuadorean locality 4). The summit of Chimborazo is hidden by clouds and a siding of the railroad from Guayaquil to Quito runs across the middle foreground. H. E. Anthony and G. H. H. Tate camped near the railroad when they collected the type series of *Sigmodon inopinatus* at this locality. Photographed in May 1916 by F. M. Chapman.

stricted to such open habitats as grass, low scrub, garden plots, and pastures. The known altitudinal range of the species extends from sea level to about 1600 m (fig. 19).

Tate summarized his observations concerning the habits of mammalian species collected in Ecuador on typewritten cards that are still filed in the AMNH Department of Mammalogy archives. On one such card he noted that *peruanus* makes distinct runways and "... is the only rat I have found that is diurnal. It comes out from two pm onwards [and] ... stays out till morning." W. H. Osgood's fieldnotes (in the FMNH Division of Mammals archives) from 30 March to 2 April 1912 at Pacasmayo (Peruvian locality 1) also imply diurnal habits and suggest that the species leaves "... green cuttings like those made by *Microtis*," but no other natural history information worthy of record is available.

***Sigmodon inopinatus*:** This species has been collected at just two localities, both at very

high elevations in the Ecuadorean Andes: near Urbina (Ecuadorean locality 4), where G. H. H. Tate and H. E. Anthony trapped twelve specimens from 24 to 26 October 1923 at about 3500 m on the eastern slopes of Chimborazo; and in Parque Nacional Las Cajas (Ecuadorean locality 1) where A. Barnett collected four specimens at 3700–3800 m in 1981, 1983, and 1984. Both collection localities lie within the *páramo*, an alpine life zone characterized by cold, humid, grass-covered hillsides and wet valley bottoms with ponds, bogs, marshes, and dense, spongy hummocks of moss. Although *páramos* are not without woody plants, trees and shrubs are minor elements in the vegetation and usually occur in discontinuous patches on sheltered hillsides and in well-drained valleys (see papers in Vuilleumier and Monasterio, 1986, for numerous references to the extensive literature on *páramo* ecology).

Anthony (1924: 4) reported only that spec-



Fig. 25. Bunch-grass and a mossy hummock, characteristic features of *páramo* vegetation; the habitat of *Sigmodon inopinatus* on the eastern slopes of Chimborazo above Urbina (Ecuadorian locality 4). Photographed in May 1916 by F. M. Chapman.

imens of *inopinatus* were collected near Urbina "... in the tufts of coarse grass which covered the paramo," and his fieldnotes are no more illuminating except to explain that

the atmosphere was too smoky for successful photography because the local people were burning the grass. Several years earlier, however, F. M. Chapman encountered more fa-

vorable atmospheric conditions, and his photographs include a general view of the *páramo* above Urbina (fig. 24), and a close-up of the vegetation (fig. 25).

Labels attached to the four specimens that A. Barnett collected in Las Cajas National Park all refer to grassy situations or to grasses mixed with shrubby Compositae, in or near marshy areas of the *páramo*.

No other data concerning the habitats or habits of this species have been recorded.

SUMMARY, COMPARISONS, AND DISCUSSION

Available information concerning the natural history of South American *Sigmodon* species suggests close resemblance with their better-known North American congeners in most important respects. As a reasonable generalization, species of *Sigmodon* can be characterized as strictly terrestrial rats that inhabit open country, cleared areas in forested regions, or wherever grass is an important component of the local vegetation. Some, and perhaps all, cotton rats are diurnal as well as nocturnal, construct runways, and subsist chiefly on the green leaves and stems of grasses and forbs. In those tropical populations studied to date, reproductive activity is apparently continuous throughout the rainy and dry seasons. Within the nonforest environments they occupy, species of *Sigmodon* are probably one of the more important lower links in the food chains that sustain vertebrate secondary consumers.

Ecological comparisons with other murid taxa encountered in the same Neotropical habitats reveal differences that suggest a distinctive trophic role for cotton rats. Of the 91 identifiable South American localities from which *Sigmodon alstoni* and/or *S. hispidus* are known, species of *Zygodontomys* have also been collected at 44, or about 48 percent (see Voss, 1991, for a gazetteer of *Zygodontomys* collection localities). *Sigmodon* and *Zygodontomys* are often taken in the same traplines or trapping grids and in apparently identical microhabitats, but where they occur together *Zygodontomys* usually appears to be the commoner taxon, or at least the more easily trapped (Aldrich and Bole, 1937; Ibáñez and Moreno, 1982; O'Connell, 1981; Vivas, 1984; Voss, 1991). Like *Sigmodon*, *Zygodontomys* is restricted to open habitats, is

strictly terrestrial, and reproduces continuously throughout the year, even in highly seasonal environments; *Zygodontomys* is also comparable to *Sigmodon* in body size (table 15) but differs by its predominantly or exclusively nocturnal activity and apparently omnivorous diet (see review by Voss, 1991). According to O'Connell (1982), *Zygodontomys* also differs from sympatric *S. alstoni* in the Llanos by not constructing runways.

Holochilus brasiliensis (sensu Hershkovitz, 1955) is found throughout the unforested lowlands of Colombia, Venezuela, and the Guianas, where it often occurs sympatrically with *Sigmodon hispidus* or *S. alstoni*. Like cotton rats, *H. brasiliensis* is predominantly herbivorous, subsisting chiefly on the green leaves and stems of grasses (including such cultivated species as sugar cane and rice), and reproduces throughout the year even where precipitation is seasonal (Twigg, 1962, 1965; Martino and Aguilera, 1989). However, *H. brasiliensis* is much larger than any species of *Sigmodon* (table 15), and is semiaquatic; its webbed hindfeet presumably facilitate aquatic locomotion in such typical habitats as seasonally inundated marshes, flooded rice fields, grassy riversides, and wet canebrakes (Hershkovitz, 1955; Twigg, 1962, 1965; Husson, 1978). Anecdotal observations suggest that *H. brasiliensis* is nocturnal (Twigg, 1962). Little ecological information is available for other muroids with which South American *Sigmodon* species may often be sympatric: *Akodon urichi*, *Calomys hummelincki*, and *Oligoryzomys fulvescens* (with *S. alstoni* and/or *S. hispidus* in Colombia and Venezuela); *Oryzomys xantheolus* (with *S. peruanus* in the western lowlands of Ecuador and Peru); and *Akodon mollis* and *Phyllotis haggardi* (with *S. inopinatus* in the Ecuadorean Andes). Nevertheless, none of these species closely resembles *Sigmodon* in features of the craniofacial skeleton and dentition that would indicate similar diets. From this observation and the preceding comparisons, it may be hypothesized that species of *Sigmodon* are the only strictly terrestrial and predominantly herbivorous muroids in the tropical ecosystems they inhabit; apparently, their closest ecological counterparts in the New World muroid fauna occupy higher latitudes. Species of *Reithrodon*, for example, inhabit the temperate grasslands of southern South

TABLE 15

Adult^a Weights (in grams) of *Sigmodon*^b and Other South American Muroids Discussed in the Text

Species	N	Weights	
		Mean \pm 1 SD	Observed range
<i>Sigmodon alstoni</i> ^c	33	67.1 \pm 15.4	37–93
<i>Sigmodon hispidus</i> ^c	43	107.5 \pm 34.8	42–184
<i>Zygodontomys brevicauda</i> ^c	46	56.7 \pm 19.4	25–105
<i>Zygodontomys brunneus</i> ^d	14	75.6 \pm 10.6	56–96
<i>Holochilus brasiliensis</i> ^e	26	155.4 \pm 58.2	59–250

^a Specimens with completely erupted molar rows are considered adults.^b Weight data are unavailable for *inopinatus* and *peruanus*.^c Specimens from various Venezuelan localities.^d Specimens from Colombian locality 12.^e Specimens from Departamento Beni, Bolivia (no adequate series are available from Colombia or Venezuela).

America where they subsist almost entirely on green vegetation (Pearson, 1988; Scaglia et al., 1982), while voles of the genus *Microtus* are the dominant small mammalian herbivores in many north-temperate grasslands (Rose and Birney, 1985). Comparisons among these and other herbivorous, grassland-dwelling rodents have provoked speculations about evolutionary convergence in behavioral, physiological, and demographic traits (Baker, 1971; Fleming, 1975; O'Connell, 1982), but such lie outside the scope of this report.

BIOGEOGRAPHY

Species of *Sigmodon* are biogeographically interesting because of their close association with open vegetation and because the genus ranges considerably north and south of the Río Atrato lowlands in northwestern Colombia, site of the last marine barrier to intercontinental dispersal of American land mammals in the Late Tertiary (Haffer, 1970). Whether the genus evolved in North America and invaded South America, or vice versa, and when, are richly speculative topics in the literature.

INTERCONTINENTAL DISPERSAL

According to Hershkovitz (1966a), muroid rodents with a complex glans penis invaded South America from Central America by overwater dispersal, perhaps as early as the Miocene, and thereafter underwent an extensive adaptive radiation in isolation from the

evolving North American fauna of muroids with simpler genitalia. In this scenario, living and fossil species of *Sigmodon* in North America are hypothesized to be descendants of a South American ancestor that dispersed back across the Bolívar seaway sometime prior to a direct land connection in the late Pliocene or early Pleistocene:

The North American range of *Sigmodon* is greater than that of any other complex-penis-type cricetine. Its present and past distribution in North America points to the cotton rat as one of the earliest overwater migrants from South America . . . Successive invasions from South America, or reinvasions of South America from Middle America, may account for the continuous distribution of living *Sigmodon hispidus* in Middle and northern South America [Hershkovitz, 1966a: 736].

Reig's (1986: 429–430) more elaborate reconstruction is also based on the assumption that *Sigmodon* evolved in South America:

Even though the Sigmodontini [an undiagnosed tribe comprising only *Sigmodon* and *Holochilus*] are now in South America a predominantly non-Andean group . . . there are strong indications that they first evolved in the North-Central Andes from a phyllotine ancestor. *Neotomys* is intermediate between phyllotines and sigmodont rodents . . . and its presence in the living fauna of the northern puna is suggestive of an origin of the genus *Sigmodon* in the pre-Pliocene Andes of northern Peru. The occurrence of *S. peruanus* . . . in the lowlands and mountain slopes west of the Andes of Ecuador and north-central Peru, and of *S. inopinatus* in the high Andes of Ecuador, is in good agreement with this hypothesis. Thus, *Sigmodon* is likely to have originated from a *Neotomys*-like ancestor in north-central Peru, and to have further dispersed westward to the western coastal lowland region of . . .

north-central Peru and Ecuador, and northward through the valleys of the Andes of Ecuador up to the proto-Magdalena Valley of Colombia, and eventually to have spread from the latter to the lowlands of Colombia and Venezuela . . . *Sigmodon inopinatus*, found isolated on the páramo of Chimborazo . . . is likely to have arrived there by the uplifting of the páramos during Plio-Pleistocene times. As a consequence of its northward spread, *Sigmodon* most probably entered Central America by overland dispersal once the Panamanian land bridge was established, some 5.5 million years ago . . . and differentiated in the arid and mesic biomes of North America into several species . . . The very primitive, $2n = 82$ karyotype . . . of *S. alstoni* suggests that its carrier is a remnant of the early *Sigmodon* differentiation, but . . . knowledge of the chromosomes of *S. peruanus* and *S. inopinatus* would be critical for this evaluation, and their karyotypes are unknown so far . . . several living North American species of *Sigmodon* have derived, low-number karyotypes. . .

To observe that these historical-biogeographic hypotheses are underdetermined by data is perhaps unnecessary. As Patterson and Pascual (1972) and many subsequent students of mammalian paleontology have observed, the earliest known South American muroid fossils are from Montehermosan (Pliocene) deposits, dated at ca. 3.5 m.y. (Marshall et al., 1979). Thus, there is no direct evidence that muroids had an extensive pre-Pliocene history in South America. A second weakness in these scenarios is the lack of compelling cladistic evidence that *Sigmodon* is closely related to any South American muroids, including other "sigmodonts" (see Phylogenetic Relationships, above). Finally, Reig's assumptions concerning primitive and derived diploid numbers in *Sigmodon* have no basis in phylogenetically defensible analyses of chromosomal evolution (and see Baker et al., 1983, for alternative views concerning plesiomorphic Neotropical muroid karyotypes).

Paleontologists, by contrast, have usually argued that *Sigmodon* evolved in North America. Fossil evidence cited to support this view is the presence of *Sigmodon* and *Prosigmodon* in late Miocene (Hemphillian) or early Pliocene (Blancan) sediments from the southwestern United States and northern Mexico (Martin, 1979; Jacobs and Lindsay, 1981; Czaplewski, 1987). The phylogenetic position of *Prosigmodon* is crucial for Jacob

and Lindsay's (1981: 428) conclusions about the historical biogeography of cotton rats:

Prosigmodon is closely related to *Calomys* (*Bensonomys*) on the one hand, and *Sigmodon* on the other. It is more advanced than *Calomys* (*Bensonomys*) while being more primitive than *Sigmodon* in height of crown, strength of connections between cusps, robustness, and development of accessory rootlets. The age of *Prosigmodon* is late Hemphillian and early Blancan. It is morphologically and temporally suited to represent a descendant of *Calomys* (*Bensonomys*). The more lingual connection of the anterocone and protocone in *Prosigmodon* relative to *Calomys* and *Sigmodon* precludes *Prosigmodon* (at least *P. oroscoi*) from direct ancestry of *Sigmodon*. However, overall similarity of *Prosigmodon* and *Sigmodon* suggests that *Prosigmodon* is near the ancestral stock of *Sigmodon* and supports the derivation of *Sigmodon* from North American cricetids,⁶ rather than from Old World cricetodontines . . . or from South American cricetids . . .

Unfortunately, virtually all North American fossil muroid taxa are known only from isolated molars, some complete tooththrows, and mandibular fragments. This material is better than nothing, but the few comparisons possible with such anatomical scraps do not encourage confidence in phylogenetic conclusions that have important biogeographic implications. Students of Recent muroid systematics routinely survey many more characters, and scepticism about the significance of the very limited morphological data presently available for most fossil taxa is not inappropriate.

Analyses of phylogenetic relationships among extant taxa could provide important data for evaluating the alternative biogeographic scenarios described above. For example, if cladistic analyses yield compelling evidence that *Sigmodon* is not closely related to the endemic South American "sigmodont" genera *Holochilus*, *Neotomys*, and *Reithrodontomys*, then much of the argument for southern ancestry evaporates. Morphological, cytological, or molecular studies to critically test "sigmodont" monophyly should minimally include representatives of all of these genera together with representative oryzomyines (a

⁶ Baskin's (1978) hypothesis that *Calomys* (*Bensonomys*) is descended from *Copemys*, a North American genus also believed to be ancestral to *Peromyscus*, is an implicit assumption of this argument.

group to which *Holochilus* may belong), phylotines (the group in which *Neotomys* and *Reithrodon* are often placed), North American genera with simple genitalia, and Old World taxa (as putative outgroups; *Calomyscus* and *Mystromys* would be good choices). Unfortunately, current morphological evidence of relationships (especially the absence of synapomorphies for the subfamily Sigmodontinae sensu either Carleton and Musser [1984] or Reig [1980]) permits no less extensive sampling design.

Different relationships among the species of *Sigmodon* are predicted by alternative biogeographic hypotheses. If the genus had a long evolutionary history in North America prior to invading South America across the newly emerged landbridge, and if South America was invaded only once, then the earliest cladogenetic events in cladistic reconstructions should be among Recent North American species, and the South American species should constitute a monophyletic group. Alternatively, if the genus evolved and speciated in South America prior to invading North America, and if the invasion was unique, then the earliest branches in cladistic reconstructions should be South American lineages, and the North American species should constitute a monophyletic group. Of course, these are the simplest alternatives and other phylogenetic results could suggest more complex biogeographic scenarios. Morphological, cytological, or molecular data sets to evaluate relationships in this context should include all of the currently recognized valid species of *Sigmodon*: *alleni*, *alstoni*, *arizonae*, *fulviventer*, *hispidus*, *inopinatus*, *leucotis*, *mascotensis*, *ochrognathus*, and *peruanus*. As emphasized earlier in this report, the genetic integrity of *hispidus* cannot be assumed, and the prudent systematist will include several samples each from North, Central, and South America. Outgroups should ideally be chosen on the basis of a prior analysis of intergeneric relationships, such as that described in the preceding paragraph.

NONFOREST MAMMAL FAUNAS AND SOUTH AMERICAN PALEOHABITATS

Because cotton rats are restricted to open habitats, the phylogenetic information ob-

tained by studies like those outlined above will be relevant for reconstructions of vegetational history as a causal factor in Neotropical faunal evolution. Webb (1978, 1991) and Marshall (1979) have postulated that savanna corridors across or around the Amazon basin connected the Llanos and other northern grasslands with grasslands on the Brazilian Shield and in Patagonia during glacial episodes in the Late Cenozoic. As noted by Voss (1991), however, savanna murid faunas north and south of Amazonia provide little evidence of former habitat continuity. If *Sigmodon* is not closely related to Patagonian or central-Andean "sigmodonts" (*Reithrodon*, and *Neotomys*), then its current distribution only in the northern nonforest regions of South America suggests that the Late Cenozoic dispersal of small, grassland-inhabiting mammals was not unimpeded, either via Webb's "high road" through the Andes or his "low road" through eastern Amazonia. If, however, *Reithrodon* and/or *Neotomys* are sister taxa of *Sigmodon*, then the presently disjunct distribution of these pastoral sigmodonts would lend additional support (to the herpetological data cited by Webb, 1978) for ancient corridors of grassland habitats.

Two species of *Sigmodon*, *hispidus* and *alstoni*, are members of a distinctive lowland fauna of nonforest mammals in northern South America that also includes *Lutreolina crassicaudata*, *Dasyppus sabanicola*, *Calomys hummelincki*, two species of *Zygodontomys*, *Cavia aperea*, and *Sylvilagus floridanus*. This fauna is most diverse in the Llanos but also occurs in adjacent but disjunct nonforest lowland regions of Colombia, Venezuela, the Guianas, and extreme northern Brazil. The occurrence of these small, nonvolant mammals in grasslands now separated by extensive tracts of rain forest has been interpreted as evidence for vicariance of pre-Recent savanna ecosystems that were probably most extensive during the last glacial maximum (Voss, 1991).

Neither *Zygodontomys* nor any other member of this northern savanna fauna, however, is known to occur sympatrically with *Sigmodon peruanus* in the nonforest lowland habitats of western Ecuador and northwestern Peru. This observation suggests

the historical absence of any grassland corridor around the northern Andes and down the west coast of South America. Presumably, the Chocó rain forests of western Colombia and northwestern Ecuador effectively isolated the lowland nonforest faunas of northern South America from those of the Pacific littoral during arid climatic phases of the Quaternary. Montane grasslands, however, perhaps resembling those now inhabited by *S. inopinatus* in the Ecuadorean Andes, might have provided ephemeral avenues for dispersal of cold-resistant taxa between the Pacific lowlands and the unforested inter-Andean valleys of Colombia.

Because these patterns of nonforest mammalian distributions broadly resemble those previously described for nonforest birds by Haffer (1967), I conclude this essay with a prediction that assumes a common cause for such zoogeographic congruence. The arid intermontane valley of the upper Río Marañón in the Amazonian catchment of northern Peru (fig. 2) is inhabited by a nonforest avifauna essentially the same as that of the dry Pacific lowlands (Chapman, 1926; Dorst, 1957; Haffer, 1967). If this fact is explained by vicariance rather than dispersal, then populations of nonforest lowland mammals closely related to Pacific littoral taxa should be expected along the upper Marañón (some of these may be members of Pearson's [1982] "grupo periandino"). Future collectors should be alert to the possible presence of cotton rats in the Marañón Valley, either *Sigmodon peruanus* or a new sister species.

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APPENDIX

List of Measured Specimens

TABLE 7

8 mi S Lake Placid: AMNH 255329, 255359, 255377, 255378, 255381–255389, 255391, 255394, 255396–255398, 255401, 255402, 255404–255406, 255408–255410, 255412–255416, 255418–255422, 255424.

TABLE 10

Valle de Suaza: USNM 541969, 542093–542104, 542106–542109, 542111–542116, 542119–542122, 542124, 542125, 542127–542134. **Minca:** AMNH 15249–15251, 15253–15255, 15259, 15260, 15263, 15264, 15270, 15273, 15278, 15281, 15283, 15284, 15286, 15287, 15489, 23227, 23238, 23240, 23243, 23245, 23248, 23251; USNM 123511, 123512. **Montalbán:** USNM 442453, 442454, 442456, 442457, 442481, 442484, 442487, 442490–442492, 442495, 442496, 442498, 442499, 442501, 442507, 442508, 442510, 442511, 442514, 442515,

442517–442520, 442523, 442525–442528, 442530, 442531, 442535, 442536, 442544–442546, 442549, 442550, 442552. **Rancho Grande:** USNM 517632, 517639, 517640, 517642, 517643, 517646, 517648, 517651–517653, 517655, 517657–517659.

TABLE 12

Rancho Grande: USNM 517660, 517661, 517663, 517666, 517667, 517669, 517670, 517672–517674, 517677–517682, 517684–517688, 517690, 517695–517698. **Hato El Frio:** AMNH 257337–257340; MHNLS 8218, 8220, 8222, 8231; USNM 448633–448640. **San Antonio Maturín:** AMNH 69757, 69762–69765, 69768, 69770, 69773–69775, 69778, 69971. **Kanuku Mountains:** AMNH 18978, 18979; BMNH 1.6.4.098, 1.6.4.100, 1.6.4.102–1.6.4.107, 1.6.4.174–1.6.4.177.

TABLE 13

Isla Puná: AMNH 19584–19586, 19588–19590, 19592, 19593, 19596, 67022, 67024, 67025, 67028–67030, 67032–67036, 67038–67043; BMNH 99.8.1.11–99.8.1.13, 99.8.1.16, 99.8.1.17, 99.8.1.61; USNM 120236, 120237. **Chongoncito:** AMNH 62967, 62968, 62971, 62972, 62974,

62978, 62981, 62984–62986, 62989, 62991, 62996, 63000, 63003, 63014. **Puente de Chimbo:** AMNH 62169, 62171, 62176, 62178, 62181, 62183, 62188, 62195, 62197, 63027–63029.

TABLE 14

Urbina: AMNH 66303, 66304, 66306–66308, 66310–66312.

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