

AN INTRODUCTION TO THE
NEOTROPICAL MUROID
RODENT GENUS *ZYGODONTOMYS*

ROBERT S. VOSS

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Frontispiece. *Zygodontomys brevicauda brevicauda*, an adult male from Hato El Frío, Estado Apure, Venezuela.

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ABSTRACT

Members of the Neotropical muroid rodent genus *Zygodontomys* are easily studied in the field and laboratory, providing opportunities for innovative research in many biological disciplines. A major impediment, however, is the confused systematics of the genus: no adequate diagnosis of *Zygodontomys* is available to permit unambiguous identifications, phylogenetic relationships to other muroids are unknown, and the species-level classification is in disarray. This monograph provides a systematic basis for future research with *Zygodontomys*, summarizes what is known concerning diverse ecological and biogeographic topics, and suggests where new investigations are most likely to yield important results.

Zygodontomys can be distinguished from other Neotropical muroids by a unique combination of morphological attributes including external proportions, mammae number, qualitative details of cranial architecture, molar occlusal morphology, molar root numbers, and characters of the viscera. Morphological comparisons among *Zygodontomys* and putatively related species in the genera *Bolomys*, *Calomys*, and *Pseudoryzomys* afford few characters suitable for phylogenetic analysis, the results of which are inconclusive by the criterion of unweighted parsimony. A broader taxonomic survey of one character, presence or absence of the gall bladder, however, reveals that the presumptive apomorphy (absence) occurs in all oryzomyines (sensu stricto) together with *Zygodontomys*, *Pseudoryzomys*, *Holochilus*, and a few other taxa; some instances of homoplasy are obvious, but the implication of recent ancestry among the above-named genera and oryzomyines (s.s.) merits the attention of future investigators.

Variation in quantitative and qualitative morphological characters among 2623 specimens of *Zygodontomys* is interpreted to reflect the existence of two species. *Z. brunneus* inhabits the intermontane valleys of the upper Río Magdalena, the upper Río Cauca, the upper Río Dagua, and the upper Río Patía in Colombia. In the upper Río Magdalena valley, *Z. brunneus* occurs sympatrically with *Z. brevicauda*, but elsewhere the two species are allopatric. The range of *Z. brevicauda* extends from the Pacific littoral of eastern Costa Rica through Panama, Colombia, Venezuela, and the Guianas, to northern Brazil. Qualitative character variation in *Z. brevicauda* reveals geographic patterns of population divergence that serve as the basis for three subspecies: *Z. b. brevicauda*, *Z. b.*

cherriei, and *Z. b. microtinus*. Insular populations of *Z. b. cherriei* in Panama and of *Z. b. brevicauda* on Trinidad and Tobago average larger in craniodental dimensions than adjacent mainland populations but are not differentiated from them in qualitative characters.

Species of *Zygodontomys* inhabit open savannas, savanna woodlands, thornscrub, shrublands, pastures, agricultural regions, and other types of natural or anthropogenic nonforest habitats on the Central and South American mainland. On some continental-shelf islands, however, *Z. brevicauda* is known to occur in closed-canopy forests. Most collection records are from elevations below 100 m, but there are numerous well-documented collections from higher altitudes, up to about 1300 m. *Z. brevicauda* is nocturnal, strictly terrestrial, and apparently omnivorous; it is numerically abundant in most suitable habitats within its ecogeographic range. Despite the dramatic seasonality of rainfall in some regions, populations of *Z. brevicauda* reproduce continuously throughout the year. Fifty-five species of arthropod ectoparasites have been collected from *Z. brevicauda* in Panama and Venezuela.

Zygodontomys is part of a nonforest vertebrate fauna with a disjunct distribution in northern South America. Other mammals that belong to this fauna include the opossum *Lutreolina crassicaudata*, the armadillo *Dasypus sabanicola*, several muroid rodents (*Calomys hummelincki*, *Sigmodon alstoni*, and *S. hispidus*), the cavy *Cavia aperea*, and the rabbit *Sylvilagus floridanus*. The occurrence of these and other flightless nonforest vertebrate species in isolated enclaves of savanna and other types of open vegetation surrounded by forests is most parsimoniously explained by vicariance. Independent evidence of paleoclimates suggests that nonforest vegetation in northern South America was more extensive during the last glacial maximum than at present, and the disjunct distributions of some modern nonforest organisms are presumably the consequence of postglacial expansions of rain forests. On this assumption, an evolutionary scenario is proposed to account for the geographic variants of *Z. brevicauda*. Some of the South American zoogeographic literature is compromised by an uncritical reliance on antiquated subspecies taxonomies, and more revisionary systematic studies will be required to serve as the basis for meaningful historical analyses of the nonforest vertebrate fauna.

RESUMEN

Los miembros del género *Zygodontomys* de roedores muroides neotropicales se estudian fácilmente en el campo y en el laboratorio, proveyendo oportunidades para investigaciones innovadoras en muchas disciplinas biológicas. Un obstáculo mayor, sin embargo, es la confusa sistemática del género: no existe una adecuada diagnosis de *Zygodontomys* que permita identificaciones claras, se desconocen las relaciones filogenéticas con otros muroides, y la clasificación a nivel de especie está en desorden. Esta monografía provee la base sistemática para futuras investigaciones con *Zygodontomys*, resume lo que se conoce en cuanto a diversos tópicos ecológicos y biogeográficos, y sugiere qué nuevas investigaciones pueden dar resultados importantes.

Zygodontomys se puede distinguir de otros muroides neotropicales por una combinación única de atributos morfológicos que incluyen las proporciones externas, el número de glándulas mamarias, detalles cualitativos de la arquitectura del cráneo, morfología oclular molar, número de raíces molares, y caracteres de los órganos internos. Las comparaciones morfológicas entre *Zygodontomys* y especies putativamente emparentadas en los géneros *Bolomys*, *Calomys*, y *Pseudoryzomys* proveyeron pocos caracteres adecuados para un análisis filogenético, los resultados del cual no fueron concluyentes por el criterio de parsimonia no ponderada. Un estudio taxonómico más amplio sobre un carácter, la presencia o ausencia de la vesícula biliar, reveló sin embargo que la presunta apomorfia (ausencia) se encuentra en todos los oryzominos (sensu stricto) junto con *Zygodontomys*, *Pseudoryzomys*, *Holochilus*, y algunos otros taxa; algunos ejemplos de homoplasias son obvios, pero las implicaciones de una ancestría reciente entre los géneros arriba mencionados y los oryzominos (s.s.) merece la atención de investigaciones futuras.

La variación en caracteres morfológicos cuantitativos y cualitativos entre 2623 especímenes de *Zygodontomys* se interpreta como que refleja la existencia de dos especies. *Z. brunneus* que habita los valles interandinos de la parte alta del Río Magdalena, la parte alta del Río Cauca, y el Río Patía en Colombia. En el valle del alto Río Magdalena, *Z. brunneus* se encuentra simpátricamente con *Z. brevicauda*, pero en el resto del área las dos especies son alopatricas. El rango de *Z. brevicauda* se extiende desde el litoral del Pacífico del este de Costa Rica cruzando Panamá, Colombia, Venezuela, y las Guayanas, al norte del Brasil. La variación de los caracteres cualitativos en *Z. brevicauda* revela patrones geográficos con divergencia de poblaciones que sirven de base para tres subespecies: *Z. b. brevicauda*, *Z. b. cherriei*, y *Z. b.*

microtinus. Las poblaciones insulares de *Z. b. cherriei* en Panamá y de *Z. b. brevicauda* de Trinidad y Tobago son más grandes en promedio en dimensiones craneodentales que las poblaciones adyacentes del continente, pero no están diferenciadas en los caracteres cualitativos.

Las especies de *Zygodontomys* habitan sabanas, matorral espinoso, arbustales, pastizales, campos agrícolas, y otros tipos de habitats abiertos naturales o antropogénicos en el continente en América del Sur y Central. Sin embargo, en algunas islas de la plataforma continental, se sabe que *Z. brevicauda* se encuentra en bosques con dosel cerrado. La mayoría de los registros de las colecciones provienen de elevaciones debajo de los 100 metros, pero hay muchas colecciones bien documentadas de altitudes mayores, hasta los 1300 metros. *Z. brevicauda* es nocturna, estrictamente terrestre, y aparentemente omnívora; es abundante en la mayoría de los habitats adecuados dentro de su rango ecogeográfico. A pesar de la dramática estacionalidad de la lluvia en algunas regiones, las poblaciones de *Z. brevicauda* se reproducen continuamente a lo largo del año. Se han colectado cincuenta y cinco especies de ectoparásitos artrópodos de *Z. brevicauda* en Panamá y Venezuela.

Zygodontomys es parte de una fauna no boscosa de vertebrados con una distribución disyunta en el norte de América del Sur. Otros mamíferos que pertenecen a esta fauna incluyen el marsupial *Lutreolina crassicaudata*, el armadillo *Dasyus sabanicola*, varios roedores muroides (*Calomys hummelincki*, *Sigmodon alstoni*, y *S. hispidus*), el cuy *Cavia aperea*, y el conejo *Sylvilagus floridanus*. La presencia de estos y otras especies de vertebrados no ocupantes de bosques y no voladores, en enclaves aislados de sabana o de otros tipos de vegetación abierta rodeados de bosque se explica más parsimoníamente por la vicarianza de los habitats anteriormente continuos. Evidencias independientes de los paleoclimas sugieren que la vegetación no boscosa en el norte de América del Sur estaba más extendida durante el último glacial máximo que en la actualidad; por lo tanto, las distribuciones modernas de algunas de las especies no boscosas son presuntamente consecuencias de las expansiones post-glaciares del bosque húmedo. Bajo esta asunción, se propone un escenario evolutivo para explicar las variaciones geográficas de *Z. brevicauda*. Algunas de los escritos en la literatura zoogeográfica de América del Sur están comprometidos por descansar acriticamente en las taxonomías anticuadas de las subespecies. Se requieren mas estudios sistemáticos de revisión para servir como base para análisis históricos significativos de la fauna neotropical de vertebrados de vegetaciones abiertas.

INTRODUCTION

Muroid rodents of the genus *Zygodontomys* are among the most abundant vertebrates in savannas and other unforested lowland habitats throughout eastern Central America and northern South America. Since their scientific discovery in 1893, species of *Zygodontomys* have been collected at hundreds of localities, and thousands of museum specimens are now available to document patterns of geographic distribution and morphological variation. Despite this numerous and accessible material, the systematic biology of the genus is not well understood.

Most taxonomic synopses of *Zygodontomys* recognize only a few of the 17 nominal taxa that it contains as valid, but alternative classifications (e.g., of Cabrera, 1961; Hershkovitz, 1962; and Reig, 1986) are unaccompanied by diagnoses or substantive discussions of character data. Tate (1939), Reig (1978), Maia and Langguth (1981), and Voss and Linzey (1981) recognized the heterogeneous contents of *Zygodontomys sensu lato*, but even after the removal of trans-Amazonian taxa (now referred to *Bolomys*), no revised morphological definition of the genus has been formulated to permit unambiguous identifications. Judgments of resemblance based on craniodental characters (Thomas, 1916; Tate, 1932b; Hershkovitz, 1962), genitalia (Hooper and Musser, 1964), and karyotypes (Gardner and Patton, 1976) have variously allied *Zygodontomys* with oryzomyines, akodonts, or phyllotines, and current suprageneric classifications of South American Sigmodontinae (e.g., Reig, 1980, 1984) list the genus as incertae sedis in recognition of its ambiguous phylogenetic affinities.

This sorry state of affairs has unfortunate consequences for researchers in many disciplines. Easily trapped, marked and recaptured in the field, and inexpensively bred in the laboratory, species of *Zygodontomys* have been included in studies of tropical grassland community ecology (e.g., August, 1984; Vivas, 1984; O'Connell, 1989), arbovirus epidemiology (Bates and Weir, 1944; Downs et al., 1962; Jonkers et al., 1964; Tikasingh et al., 1966), reproductive physiology (Heide-man and Bronson, 1990), and biometrical

genetics (Voss et al., 1990; Voss and Marcus, in prep.). Effective communication of forthcoming research results requires a meaningful taxonomic framework for information retrieval, and comparisons with studies of other muroid taxa would be enhanced by well corroborated hypotheses of phylogenetic relationships. The present report provides a systematic foundation for ongoing biological research with *Zygodontomys*, summarizes existing natural history information about these animals, and outlines some of the biogeographic interpretations that follow from the results of systematic and ecological research. This monograph is an introduction to *Zygodontomys*: a preliminary synthesis of information and a source of hypotheses that should be tested by subsequent researchers using other materials and methods.

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The "we" employed throughout my descriptions of fieldwork in *Zygodontomys* habitats includes many colleagues who worked hard under sometimes trying circumstances to help collect specimens and ecological data: Ken Creighton (Costa Rica, 1984); Helen Kafka, Hernán Castellanos, Isa Torrealba, José Ayarzagüena, Giuseppe Colonnello, Carlos Lasso, and Pablo Morales (Venezuela, 1986); Hernán Castellanos, Carlos Gauveca,

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Three uniquely talented artists have par-

ticipated in the production of this report. Pat Wynne drew figures 1–3, 8–13, 16, 18, 19, 21–23, 25–30, and 36–40; each is testimony to her discerning eye, agile pen, and commitment to elegant scientific illustration. Fran Stiles painted the frontispiece with her characteristic attention to anatomical details and nuances of posture that bring the image to life. Peter Goldberg photographed the skulls in figures 5 and 17, and printed the habitat photographs in figures 31–35; the exceptional clarity of these images is the result of his skillful and painstaking darkroom efforts.

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MATERIALS AND METHODS

SPECIMENS

This report is based on 2623 specimens of *Zygodontomys*, consisting of skins, skulls, postcranial skeletons, and fluid-preserved material deposited in the following collections: the American Museum of Natural History, New York (AMNH); the British Museum (Natural History), London (BMNH); the Colección de Mamíferos de INDERENA, Bogotá (CMIND); the Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); the Field Museum of Natural History, Chicago (FMNH); the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); the Los Angeles County Museum of Natural History, Los Angeles (LACM); the Louisiana State University Museum of Zoology, Baton Rouge (LSU); the Ministerio del Ambiente y de los Recursos Naturales Renovables, Maracay (MARNR); the Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); the Museo de Historia

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Information provided under the heading "Specimens Examined" in the species and subspecies accounts consists of the number of preparations from which data were recorded, listed by museum collection, for each

locality. Catalog numbers are provided in Appendix I for specimens whose measurements are summarized by statistics tabulated in the text.

COLLECTION LOCALITIES

I was able to determine the approximate geographic coordinates of 230 localities from which specimens of *Zygodontomys* have been collected. Italicized proper names in the list below are of the largest administrative units (states, departments, provinces, etc.) recognized within each country; boldface identifies locality names as they are used in the text of this report. Latitude (degrees and minutes North) and longitude (degrees and minutes West) are given in parentheses without punctuation (e.g., 0048/6714 for 0°48'N, 67°14'W) after the most restrictive place name for which they could be determined. References that I consulted in compiling this information included publications of the United States Central Intelligence Agency (NIS gazetteers for Brazil, Colombia, Costa Rica, the Guianas, Panama, and Venezuela), Fairchild and Handley (1966), Handley (1976), Husson (1978), Paynter and Traylor (1981), Paynter (1982), Stephens and Traylor (1985), a variety of maps, and unpublished materials. Elevations are reported verbatim (in feet or meters) from specimen labels and field notes, or from cited secondary sources. Localities, numbered consecutively within countries, are mapped in figures 1 and 2.

BRAZIL

1. *Amazonas*, **Tabocal** (0048/6714), Rio Negro; elevation less than 100 m (from map).
2. *Pará*, **Serra do Tumucumaque**, 12 km da Guiana Holandesa (ca. 0230/5600).
3. *Roraima*, **Limão** (0356/6030) on the Rio Coitinga; elevation about 1500 ft (Tate, 1939).
4. *Roraima*, **Serra da Lua**, ca. 60 mi SE Boa Vista (0251/6043); this locality is presumed synonymous with the "Moon Mountains" of British collectors; the range is also labeled as the "Kai-Irite" mountains on old maps.

COLOMBIA

1. *Antioquia*, 11–12 km S **Caucasia** (0800/7512); elevations from 200 to 250 m.
2. *Antioquia*, 11 km S and 30 km E **Cisneros** (0633/7504).

3. *Antioquia*, **San Jerónimo**, 35 km NW Medellín (0627/7545); elevations from 720 to 800 m.
4. *Atlántico*, **Ciénaga de Guájaro**, near Sabana Larga (1038/7455); elevation 15 m (Hershkovitz, 1950).
5. *Bolívar*, 1 km NW **Boquillas** (0907/7434); elevation less than 100 m (from map).
6. *Bolívar*, **Norosi** (0832/7402), Mompós; elevation 120 m (Hershkovitz, 1977).
7. *Bolívar*, **San Juan Nepomuceno** (0957/7505), elevation 167 m.
8. *Boyacá*, **Muzo** (0532/7406); elevations from 850 to 1300 m.
9. *Casanare*, Municipio Maní, **Finca Balmoral** (0455/7223); elevation less than 500 m (from map).
10. *Cauca*, **Patía**, Inspección de Policía Galíndez (0156/7708); elevations between 500 and 1000 m (from map).
11. *Cauca*, **Río Guachicón** (0156/7708); elevation 650 m.
12. *Cesar*, **El Orinoco** (1010/7324), Río Cesar, Valledupar; elevation 158 m (Hershkovitz, 1950).
13. *Cesar*, **Río Guaimaral**, near Aguas Blancas (1014/7330); elevation 140 m (Hershkovitz, 1950).
14. *Cesar*, **San Alberto** (ca. 0749/7340), Magdalena; elevation 350 m.
15. *Chocó*, **Unguía** (0801/7704), including upper Río Ipetí; elevations from sea level to 50 m.
16. *Córdoba*, **Montería** (0846/7553), Granja Turipana; elevation less than 100 m (from map).
17. *Córdoba*, **Socorré** (0751/7617), upper Río Sinú; elevation 100 m.
18. *Cundinamarca*, **Caparrapi** (0521/7430), Los Volcanes; elevation about 1250 m (from map).
19. *Cundinamarca*, **Paime** (0522/7410), elevation 1038 m (Paynter and Traylor, 1981).
20. *Guajira*, **Villanueva** (1037/7259); elevation 274 m (Hershkovitz, 1950).
21. *Huila*, **Andalucía** (ca. 0154/7540), and adjacent localities in **Valle de Suaza**; elevation 3000 ft at Andalucía.
22. *Huila*, vicinity of **Villavieja** (0313/7514); elevations from 1400 to 1600 ft.
23. *Magdalena*, **Bonda** (1114/7408) and nearby localities **Mamatoco**, **Masinga Veija**, and **Santa Marta**; elevations from sea level to 600 ft (Allen, 1904).
24. *Magdalena*, **Isla de Salamanca** (1058/7430), 0.5 km W Los Cocos; sea level (Paynter and Traylor, 1981).
25. *Meta*, **Fuente de Oro** (0328/7337), vereda La Esperanza, Finca La Virginia; elevation between 200 and 500 m (from map).
26. *Meta*, vicinity of **Puerto Gaitán** (ca. 0418/7205); elevation less than 200 m (from map).
27. *Meta*, **Puerto Lopez** (0405/7258); vereda Menegua, Finca El Lagunazo; elevation less than 200 m (from map).

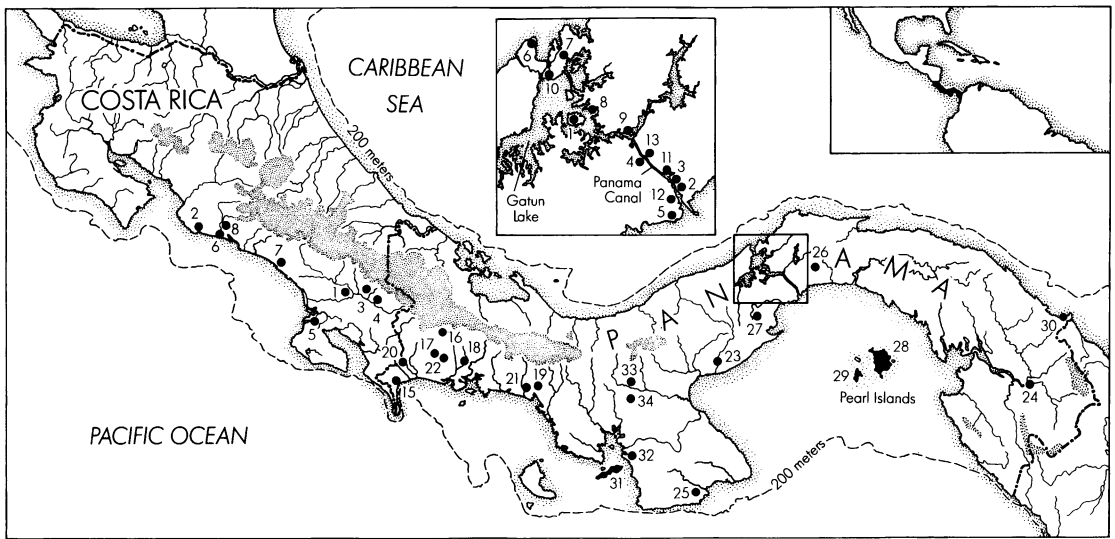


Fig. 1. Collection localities in Central America. Densely stippled land areas are those over 1500 m elevation. Names and geographic coordinates of numbered localities are provided in the text.

28. *Meta*, **Puerto Lleras** (0316/7323); elevation less than 500 m (from map).

29. *Meta*, **Restrepo** (0415/7333); elevation 600 m.

30. *Meta*, **San Juan de Arama** (0326/7350), including Los Micos; elevation between 500 and 1000 m (from map).

31. *Meta*, **San Martín** (0342/7342); elevation 422 m (Paynter and Traylor, 1981).

32. *Meta*, vicinity of **Villavicencio** (0409/7337), including Finca El Buque; elevations from 500 to 600 m.

33. *Nariño*, **Finca Arizona**, 4.5 km S Remolino (0217/7828); elevation between 500 and 1000 m (from map).

34. *Norte de Santander*, **El Guayabal** (0801/7230), 10 mi N Cúcuta; elevation ca. 200 m (Paynter and Traylor, 1981).

35. *Santander*, **Hacienda Montebello** (ca. 0700/7325), near Cerro San Pablo; elevation 350–500 m (Hernández-Camacho, 1957).

36. *Sucre*, **Colosó** (0930/7521), Las Campanas; elevation 200 m (Paynter and Traylor, 1981).

37. *Tolima*, **Chicoral** (0413/7459); elevation 1800 ft.

38. *Tolima*, **El Triunfo** (misspelled “El Triunfo” by Allen, 1913), near Honda (0512/7445); elevation 600 ft.

39. *Valle de Cauca*, vicinity of **Cali** (0327/7631).

40. *Valle de Cauca*, Municipio Dagau, **Atuncela** (0346/7642) and 1.5 km S **Loboguerrero** (0346/7641); elevations from ca. 700 to 800 m.

41. *Valle de Cauca*, Municipio Ansermanuevo (0448/7559), **Hacienda Formosa**; elevation ca. 930 m.

42. *Vichada*, **Maipures** (0511/6749); elevation 115 m (Paynter and Traylor, 1981).

43. *Vichada*, vicinity of **Puerto Carreño** (0612/6722); elevation 100 m (Paynter and Traylor, 1981).

44. *Vichada*, **Territorio Faunístico “El Tuparro”** Centro Administrativo (ca. 0520/6748); elevation less than 100 m (from map).

COSTA RICA

1. *Puntarenas*, **Boruca** (0900/8320); elevation 1600 ft (Goodwin, 1946).

2. *Puntarenas*, **Esterillos Oeste**, 15 km SE Jaco (0936/8437); elevation less than 100 m (from map).

3. *Puntarenas*, **Finca Helechales** (0905/8305); elevation 910 m.

4. *Puntarenas*, **Gromaco**, 15 km ESE Portrero Grande (0900/8311); elevation 1100 ft.

5. *Puntarenas*, **Palmar** (0858/8329) and 12 mi SSW Palmar Sur (0858/8329); elevation less than 100 m (from map).

6. *Puntarenas*, **Parrita** (0930/8419) including Finca Ligía; elevation less than 100 m (from map).

7. *Puntarenas*, 2 km W **Rio Barú**, including Dominical (0913/8351) and vicinity; elevation less than 100 m (from map).

8. *Puntarenas*, **Sardinal** (ca. 0932/8419); elevation less than 100 m (from map).

FRENCH GUIANA

1. **Bellevue** near Iracoubo (0529/5313); sea level (Stephens and Traylor, 1985).

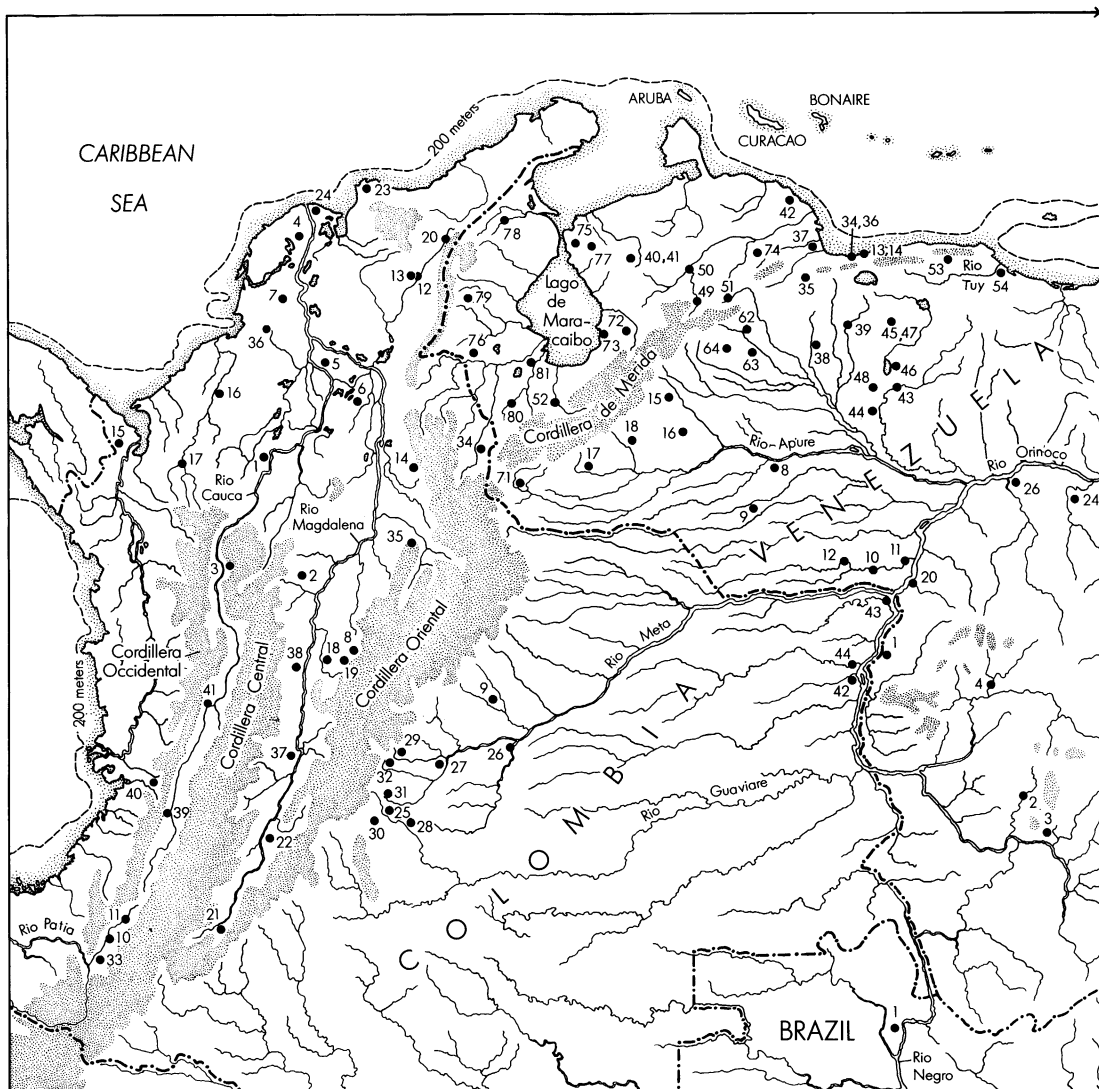


Fig. 2. Collection localities in South America. Densely stippled land areas are those above 1500 m elevation. Names and geographic coordinates of numbered localities are provided in the text.

2. **Cacao** (0435/5228); elevation 24 m (Stephens and Traylor, 1985).
3. **Cayenne** (0456/5220) including Roche Marie and Rorota; sea level (Stephens and Traylor, 1985).
4. **Kourou** (0509/5239); sea level (Stephens and Traylor, 1985).
5. **Piste de St. Elie**, km 16 (between Fleuve Sinnamary [ca. 0453/5300] and Saint-Elie [0450/5317]); sea level (Stephens and Traylor, 1985).

GUYANA

1. **East Demerara-West Coast Berbice, Great Falls** (0519/5831); elevation 27 m (Stephens and Traylor, 1985).

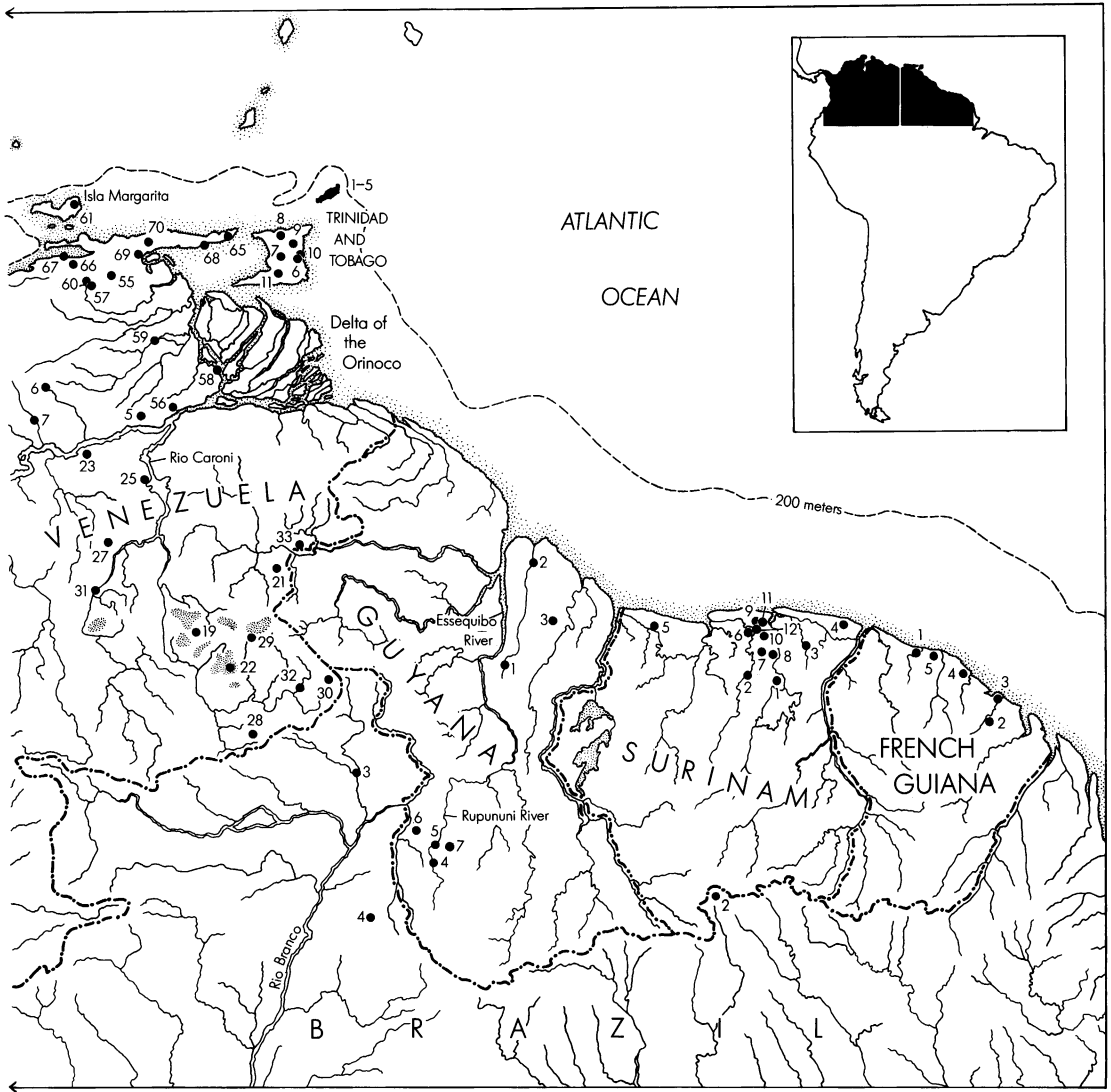
2. **East Demerara-West Coast Berbice, Hyde Park** (0630/5816); elevation less than 100 m (from map).

3. **East Demerara-West Coast Berbice, Tauraculi** (0557/5748); 65 mi up Abary River; elevation less than 100 m (from map).

4. **Rupununi, Dadanawa** (0250/5930); elevation less than 200 m (from map).

5. **Rupununi, Kanuku Mountains** (ca. 0312/5930), including J. J. Quelch's localities "Rupununi River," "Upocarit," "Kwaimatta" (or "Kwaimattat"), "Wainu," and "Tewa-Kewa"; elevations from 200 to 600 ft.

6. **Rupununi, Nappi Creek** near Letham (0323/



5948), Kanuku Mountains; elevation less than 200 m (from map).

7. *Rupununi, Weri More* (no coordinates or elevation available).

[For "Moon Mountains," a locality sometimes attributed to British Guiana, see Brazilian locality "Serra da Lua."]

PANAMA

1. *Canal Zone, Barro Colorado Island* (0909/7951); elevation between 85 and 537 ft (Enders, 1935).

2. *Canal Zone, Corozal* (0859/7934).

3. *Canal Zone, Curundu* (0859/7933) and *Fort Clayton* (0901/7934); elevation less than 100 m (from map).

4. *Canal Zone, Empire* (0904/7940).

5. *Canal Zone, Fort Kobbe* (0855/7935); elevation less than 100 m (from map).

6. *Canal Zone, Fort Sherman* (0922/7957) and *Camp Piña* (0916/8000) or "Piña Artillery Range"; elevation ca. 5 m (Fleming, 1970).

7. *Canal Zone, France Field* (0921/7953) or "France AFB"; elevation less than 100 m (from map).

8. *Canal Zone, Frijoles* (0910/7949); elevation less than 100 m (from map).

9. *Canal Zone, Gamboa* (0906/7942); elevation less than 100 m (from map).
10. *Canal Zone, Gatún* (0915/7956); elevation less than 100 m (from map).
11. *Canal Zone, Red Tank* (0900/7936); elevation less than 100 m (from map).
12. *Canal Zone, Rodman Naval Ammo Depot* (0856/7935); elevation 50 m (Fleming, 1970).
13. *Canal Zone, Summit* (0903/7940); elevation less than 100 m (from map).
14. *Canal Zone, Tabernilla* (0907/7949), now beneath Gatun Lake, near Barro Colorado Island; elevation less than 100 m (from map).
15. *Chiriquí, Armuelles* (0817/8252); elevation less than 100 m (from map).
16. *Chiriquí, El Banco* (0842/8231); elevation ca. 3500 ft (Fairchild and Handley, 1966).
17. *Chiriquí, Boquerón* (0831/8234); elevation less than 200 m (from map).
18. *Chiriquí, El Valle* (0826/8220); elevation less than 100 m (from map).
19. *Chiriquí, Guabalá* (0813/8144).
20. *Chiriquí, Progreso* (0827/8250); elevation less than 100 m (from map).
21. *Chiriquí, 1 mi E Remedios* (0814/8151); elevation 200 ft.
22. *Chiriquí, 2 mi W San Juan* (ca. 0828/8229).
23. *Coclé, Antón* (0824/8016); elevation less than 100 m (from map).
24. *Darién, El Real* (0806/7745); elevation less than 100 m (from map).
25. *Los Santos, Guánico Arriba* (0720/8030).
26. *Panamá, Cerro Azul* (0914/7921, as "La Zumbadora" in Fairchild and Handley, 1966); elevation 2000 ft (Handley, 1966).
27. *Panamá, El Aguacate* (0845/7958); elevation ca. 1000 ft (Tesh, 1970).
28. *Panamá, San Miguel Island* (= Isla del Rey, 0823/7856); elevation probably less than 100 m (from map).
29. *Panamá, Isla San José* (0815/7908); elevation probably less than 100 m (from map).
30. *San Blas, Armila Village* (0840/7727), including "Quebrada Venado"; sea level.
31. *Veraguas, Isla Cébaco* (0731/8111); elevation less than 300 m (from map).
32. *Veraguas, Mariato, 1.5 mi E Montijo Bay, Paracoté* (0740/8101); elevation 50 ft (Aldrich and Bole, 1937).
33. *Veraguas, 2 mi S San Francisco* (0815/8058); elevation 200 ft.
34. *Veraguas, Santiago* (0805/8059).

SURINAM

1. *Brokopondo, Berg en Dal* (0509/5504), W bank Suriname River, 75 km S Paramaribo; elevation less than 250 m (from map).
2. *Brokopondo, Finisanti* (0508/5529) and *Loksiehatti* (0509/5528); elevation less than 250 m (from map).
3. *Commewijne, Gododrai* (0528/5441), upper Comewijne River; elevation less than 250 m (from map).
4. *Marowijne*, between Moengotapoe (0535/5415) and the coast near *Wiawia Bank* (0558/5421), 0.5 to 2.5 km from coast; sea level (Stephens and Traylor, 1985).
5. *Nickerie, Wageningen* (0546/5641) and vicinity; sea level (Stephens and Traylor, 1985).
6. *Saramacca, Dirkshoop* (ca. 0546/5528) and *La Poule* (ca. 0546/5527); elevation less than 250 m (from map).
7. *Saramacca, Matta* (0528/5521), 15 km W Zanderij Airport; elevation less than 250 m (from map).
8. *Suriname, Carolina Kreek* (0525/5510); elevation less than 250 m (from map).
9. *Suriname, Garnizoenspad*, 19 km W Paramaribo (0550/5511) and *Kwatta* (0551/5518; about 10 km W Paramaribo); sea level (Stephens and Traylor, 1985).
10. *Suriname, Lelydorp* (0542/5516) and *Lelydorpplan* (0540/5512); elevation less than 250 m (from map).
11. *Suriname, Paramaribo* (0550/5511), including Cultuurtuin (Agricultural Experimental Station), and Plantation Clevia (ca. 8 km NE Paramaribo); near sea level (Stephens and Traylor, 1985).
12. *Suriname/Saramacca, Uitkijk* (0546/5520); elevation less than 250 m (from map).

TRINIDAD AND TOBAGO

1. *Tobago*, vicinity of *Charlotteville* (1119/6033) including Pigeon Peak (1118/6033); elevations from 25 to 570 m.
2. *Tobago*, near intersection of *Lambeau Hill Crown Trace and Windward Road* (ca. 1117/6032 at Lambeau Hill).
3. *Tobago, Richmond* (ca. 1113/6036); elevation ca. 100 ft (from map).
4. *Tobago, 4.5 km N Roxborough* (1115/6035), Roxborough Valley.
5. *Tobago, Speyside* (1118/6032); elevation ca. 100 ft or less (from map).
6. *Trinidad, Bush Bush Forest* (1024/6103), N-riva Swamp; elevation ca. 10 ft (Downs et al., 1968).
7. *Trinidad, Caparo* (1027/6120); elevation 150 ft (Goodwin and Greenhall, 1961).
8. *Trinidad, Caura* (1043/6121); elevation 600 ft (Goodwin and Greenhall, 1961).
9. *Trinidad, Sangre Grande* (1035/6107) including Maingot Estate, Rio Grande Forest, and Or-

opouche (1036/6106); elevations from 50 to 1200 ft.

10. *Trinidad, North Manzanilla* (1031/6102); elevation 50 ft (Goodwin and Greenhall, 1961).

11. *Trinidad, Princes Town* (1016/6123); elevations from 100 to 150 ft (Goodwin and Greenhall, 1961).

VENEZUELA

1. *Amazonas, Estación Experimental Amazonas, near Atures* (ca. 0535/6736); elevation less than 100 m (from map).

2. *Amazonas, Belén* (0339/6546) Río Cunucunuma; elevation 150 m (Handley, 1976).

3. *Amazonas, Esmeralda* (0310/6533), near Cerro Duida; elevation 135 m (Handley, 1976).

4. *Amazonas, San Juan Manapiare* (0518/6613); elevation 155 m (Handley, 1976).

5. *Anzoátegui, Mamo* (0828/6302); elevation less than 100 m (from map).

6. *Anzoátegui, Río Caris* (Los Cocos), 37 km SW El Tigre (0855/6415); elevation less than 500 m (from map).

7. *Anzoátegui, Río Pao*, Hacienda San Antonio, 52 km S El Tigre (0855/6415); elevation less than 500 m (from map).

8. *Apure, Hato El Frío*, 31 km (by road) W El Samán de Apure (0755/6844); elevation about 60 m.

9. *Apure, Hato La Trinidad de Arauca* (ca. 0711/6904); elevation less than 100 m (from map).

10. *Apure, 41 km NW Puerto Paez* (0613/6728), Río Cinaruco; elevation 76 m.

11. *Apure, 60 km NE Puerto Paez* (0613/6728); elevation 76 m.

12. *Apure, 95–115 km NW Puerto Paez* (0613/6728), Río Cinaruco; elevation less than 100 m (from map).

13. *Aragua, vicinity of Ocumare de la Costa* (1028/6746); elevation less than 40 m (from map).

14. *Aragua, Bahía de Cata* (1030/6744) near Ocumare de la Costa; elevation 50 m.

15. *Barinas, vicinity of Barrancas* (0846/7006), including El Caimital and Estación Experimental El Irei; elevations from 170 to 220 m.

16. *Barinas, Hato La Candelaria*, 40 km SE Barinas (0838/7012); elevation 100 m.

17. *Barinas, 8 km SW Santa Barbara* (0747/7110); elevation less than 500 m (from map).

18. *Barinas, Ticoporo*; elevation 100 m.

19. *Bolívar, Auyánteupui* including Uruyén (0541/6226, also spelled "Hurulleng") and Camarata Valley; elevation 460 m and 1100 m (see map in Tate, 1938).

20. *Bolívar, Boca de Parguaza* (0624/6712); elevation less than 100 m (from map).

21. *Bolívar, Camp Mop*, km 38 S El Dorado (0644/6138).

22. *Bolívar, Churi-Tepui* (0513/6154); elevation 6400 ft.

23. *Bolívar, 29 km WSW Ciudad Bolívar* (0808/6333); elevation 100 m.

24. *Bolívar, El Llagual* (ca. 0725/6510), on lower Río Caura near Maripa; elevation less than 500 m (from map).

25. *Bolívar, El Mirador, Represa de Guri* (ca. 0741/6255); elevation 200 m.

26. *Bolívar, Hato La Florida* (ca. 0727/6546), 44–53 km SE Caicara (0737/6610); elevation from 43 to 68 m (Handley, 1976).

27. *Bolívar, Hato San José*, 20 km W La Paragua (0650/6320); elevations from 297 to 309 m (Handley, 1976).

28. *Bolívar, 46–54 km NE Icabarú* (0420/6145), *Cumbre del Abismo* (ca. 0423/6141), and *Morichal Aguas Negras* (ca. 0420/6140); elevations from 905 to 960 m.

29. *Bolívar, Kavanayén* (0538/6148); elevation 3100 ft.

30. *Bolívar, Roraima*, including Arabopó (also spelled "Arabupu"; 0506/6044) and Paulo (see map in Tate, 1930); elevations from 4000 to 4200 ft.

31. *Bolívar, Salto Uraima* (0617/6335), Río Paragua; elevation less than 500 m (from map).

32. *Bolívar, San Ignacio Yuruaní* (ca. 0502/6108); elevations from 860 to ca. 900 m.

33. *Bolívar, San Martín Turumbán* (ca. 0643/6107); elevation less than 500 m (from map).

34. *Carabobo, Hacienda Saint Jean*, 2 km SE, and 13 km SW Borburata (1026/6758); elevations from 40 to 120 m.

35. *Carabobo, vicinity of Montalbán* (1013/6820); elevations from 579 to 598 m.

36. *Carabobo, Patanemo* (1026/6755), including Ensenada Yapascua (1028/6754) and vicinity; elevations from 0 to 50 m.

37. *Carabobo and Yaracuy*, 10–19 km NW Urama (1027/6819); elevation 25 m.

38. *Cojedes, Hato Itabana*, 38 km SE Las Vegas (0935/6837); elevation less than 500 m (from map).

39. *Cojedes, Hato Nuevo* (0912/6805), ca. 70 km SE Tinaco; elevation less than 500 m (from map).

40. *Falcón, Cerro Socopo* (1028/7048); elevation 1260 m.

41. *Falcón, Hacienda Socopito* (1030/7044); elevations from 470 to 480 m.

42. *Falcón*, 5 km N and 13 km E Mirimire (1110/6843); elevation 90 m.

43. *Guárico, Estación Biológica de los Llanos* (0852/6723); elevations from 100 to 115 m (Handley, 1976).

44. *Guárico, Hato La Fe*, near Corozo Pando (0830/6735); elevation 90 m.

45. *Guárico, Hato Las Palmitas* (0936/6727), 34 km S and 12 km W San Juan de los Morros; elevation 181 m.
46. *Guárico, Hato Los Leones* (0903/6716), Caño Agua Fria, 23 km NE Calabozo; elevation 88 m.
47. *Guárico, Hato Mata de Bejuco*, Parapara de Ortiz (0944/6718); elevation less than 500 m (from map).
48. *Guárico, Parcela 200*, about 20 km SW Calabozo (0856/6726) on road to San Fernando Apure; elevation less than 500 m (from map).
49. *Lara, 10 km N El Tocuyo* (= "Caserio Boro" of Handley, 1976; El Tocuyo is at 0947/6948); elevation 537 m.
50. *Lara, Río Tocuyo* (1016/6956); elevation 500 m.
51. *Lara*, vicinity of *San Miguel* (0953/6931), including San Gerónimo and La Fortuna; elevations from 960 to 980 m.
52. *Mérida, El Vigía* (0838/7139); elevation 150 m.
53. *Miranda, 19 km E Caracas* (1030/6655).
54. *Miranda, Río Chico* (1019/6558); elevation 1 m (Handley, 1976).
55. *Monagas*, vicinity of *Caripe* (1012/6329); elevations from 860 to 1180 m.
56. *Monagas, 20 km SE Chaguaramas* (ca. 0837/6245); elevation less than 100 m (from map).
57. *Monagas, Guana Guana* (1005/6336); elevation 420 m.
58. *Monagas, Isla Guara*, opposite Tucupita (ca. 0904/6205); elevation less than 100 m (from map).
59. *Monagas, Hato Mata de Bejuco*, 47–76 km SE Maturín (0945/6311); elevations from 18 to 36 m.
60. *Monagas and Sucre, Río Cocollar* (ca. 1010/6347), *San Antonio Maturín* (1007/6343), and *Campo Alegre* (ca. 1010/6345); elevations from 1350 to 2600 ft.
61. *Nueva Esparta, Cerro Matasiete*, 2 km N and 2 km E La Asunción (1102/6353; = "Isla Margarita" of Handley, 1976); elevations from 405 to 420 m.
62. *Portuguesa*, vicinity of *Acarigua* (0933/6912); elevation less than 500 m (from map).
63. *Portuguesa, Colegio Agrícola Turén* (ca. 0920/6906); elevation 120 m.
64. *Portuguesa, Tierra Buena*, near Ospino (0918/6927); elevation less than 500 m.
65. *Sucre, Cristóbal Colón* (= "Macuro" at 1039/6156, according to Paynter, 1982); elevation 1500 ft.
66. *Sucre, Cuchivano* (ca. 1015/6355), *Cumana-coa* (1015/6355), and *Quebrada Seca* (misspelled "Quebara Seca" or "Quebrada Seca"; 1018/6357 as "Villaroel" in Paynter, 1982); elevations all about 700 ft.
67. *Sucre, 11–24 km E Cumaná* (1028/6410); elevations from sea level to 20 m.
68. *Sucre, Ensenada Cauranta* (1038/6215), 7 km N and 5 km E Guiria; elevations from 4 to 7 m.
69. *Sucre, Finca Vuelta Larga*, 9.7 km (by road) SE Guaraúnos (1033/6307); elevation 10 m.
70. *Sucre, Manacal* (1037/6301), 5 km S and 25 km E Carupano; elevations from 410 to 495 m.
71. *Táchira, Estación Experimental Santa Rosa-Santo Domingo* (ca. 0734/7205); elevation 300 m.
72. *Trujillo, El Dividive* (0929/7044), 28–30 km NW Valera (= "Valera" of Handley, 1976); elevation 90 m.
73. *Trujillo, 52 km WNW Valera*, near *Santa Apolonia* (= "La Ceiba" of Handley, 1976; 0928/7104); elevations from 29 to 39 m.
74. *Yaracuy, Finca El Jaguar*, 15 km NNW Aroa (1026/6854); elevation 820 m.
75. *Zulia, El Panorama* (ca. 1040/7125), Río Aulare; elevation less than 100 m (from map).
76. *Zulia, El Rosario* (ca. 0909/7236), 45 km WNW Encontrados; elevation 37 m.
77. *Zulia, Empalado Savanna*, ca. 30 mi E El Panorama (ca. 1040/7125); elevation about sea level.
78. *Zulia, Hacienda Rodeo*, 18 km N and 56 km W Maracaibo (near "Cerro Azul" of Handley, 1976; 1051/7216); elevation 80 m.
79. *Zulia, Misión Tukuko* (0950/7252); elevation 200 m.
80. *Zulia, Morotuto* (ca. 0824/7159); 40 km SSW Santa Cruz; elevation less than 100 m (from map).
81. *Zulia, 5 km N San Carlos de Zulia*; elevation less than 100 m (from map).

MEASUREMENTS

External dimensions are not generally useful for distinguishing species or subspecies of *Zygodontomys*, and the only external measurement included in this report is hindfoot length (HF). I measured length of the hindfoot (including claws) to the nearest millimeter on study skins using dial calipers. Undistorted, dried hind feet usually yield measurements that are within one millimeter (plus or minus) of values determined from fresh specimens.

I measured skulls and teeth with dial calipers to the nearest 0.05 mm, but values are reported here only to the nearest 0.1 mm (data recorded to two decimal places are desirable in some statistical contexts, but such accuracy is superfluous for the simpler descriptive purposes of the present study). The 12 cranial dimensions measured are defined below, following their standard abbreviations, and are illustrated in figure 3.

CIL, condylo-incisive length: Measured from the greater curvature of an upper incisor to the ar-

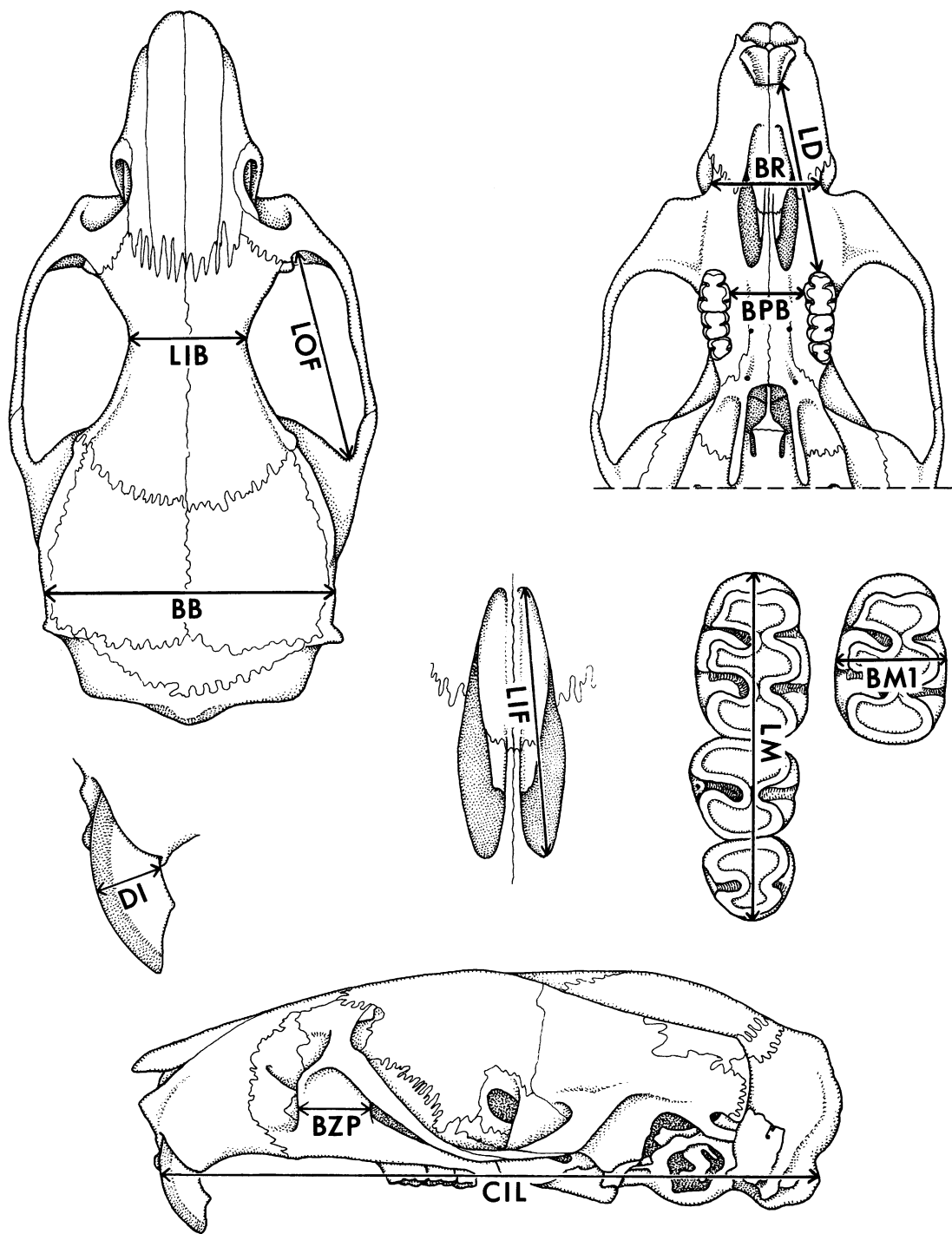


Fig. 3. Limits of 12 craniodental measurements defined in the text.

ticular surface of the occipital condyle on the same side.

LD, length of diastema: Measured from the crown of the first maxillary molar to the exposed lesser curvature of the upper incisor on the same side.

LM, length of molars: Occlusal length of the maxillary molar row.

BM1, breadth of M1: Breadth of the first molar across the protocone-paracone cusp pair.

LIF, length of incisive foramen: Inside length of one incisive foramen.

BR, breadth of rostrum: Measured just inside the anteroventral edge of the zygomatic plate.

BPB, breadth of palatal bridge: Measured between the protocones of the first maxillary molars.

BZP, breadth of zygomatic plate: Least distance between anterior and posterior edges of the zygomatic plate.

LIB, least interorbital breadth: Least distance across the frontal bones between the orbital fossae.

BB, breadth of braincase: Measured immediately dorsal to the squamosal roots of the zygomatic arches and ventral to the temporal ridges.

DI, depth of incisor: Distance between greater and lesser curvatures of an upper tooth.

LOF, length of orbital fossa: Greatest dimension of the orbital fossa inside the maxillary and squamosal roots of the zygomatic arch.

AGE CRITERIA

Young *Zygodontomys* have a dull, woolly, immature pelage that is replaced by a mature coat when the animals are still very small. Since basicranial sutures remain open throughout life, the only remaining criterion on which to base a useful age classification is molar toothwear. Five stages of dental attrition (TWC = toothwear class) are defined below and examples are illustrated in figure 4.

TWC 1: M3 incompletely erupted or unworn.

TWC 2: M3 fully erupted and exhibiting slight to moderate wear (some dentine exposed), but the occlusal surface still tubercular (the paracone raised and prominent), not flat.

TWC 3: M3 well worn, the occlusal surface flat or concave; M1-2 tubercular (the major cusps all separate and prominent); anteroloph of M2 distinct, not fused with paracone.

TWC 4: M3 flat or concave; M1-2 with cusps worn almost or quite flat but not

below widest part of crown; anteroloph of M2 obliterated, fused with paracone.

TWC 5: M1-3 all worn flat or concave, below widest part of crowns; most details of occlusal topography obliterated.

Complete eruption of the molar dentition roughly coincides with sexual maturation and completion of the postjuvenile molt. Throughout the text of this monograph, animals with an incompletely erupted molar dentition (TWC 1) are therefore referred to as "juveniles," animals in TWC 2-4 as "adults," and animals in TWC 5 as "old adults."

ANATOMICAL NOMENCLATURE AND METHODS

Considerable anatomical detail is described here using nomenclature that will be familiar to most muroid systematists. Anatomical terms that are not explained or illustrated follow usages established or referenced by Reig (1977), Wahlert (1985), and Voss (1988). Anatomical methods are standard: dissections are of specimens fixed in formalin and later stored in 70 percent ethanol; electron micrographs are of specimens sputter-coated with gold-palladium.

MULTIVARIATE STATISTICAL METHODS

I used cluster analysis and principal components analysis to display multivariate patterns of morphometric similarity among conspecific samples. The distance metric of choice for biological interpretation of correlated measurement characters is generalized (Mahalanobis) distance (Lerman, 1965), which expresses sample mean differences in units of within-sample standard deviations. Applications of this statistic assume that sample dispersions are similar except in location, a requirement that is approximately satisfied by log-transformed craniodental measurement data from sufficiently large and homogeneous samples of *Zygodontomys* (Voss et al., 1990). Multivariate normality is not a necessary assumption for meaningful interpretation of Mahalanobis distances (Mitchell

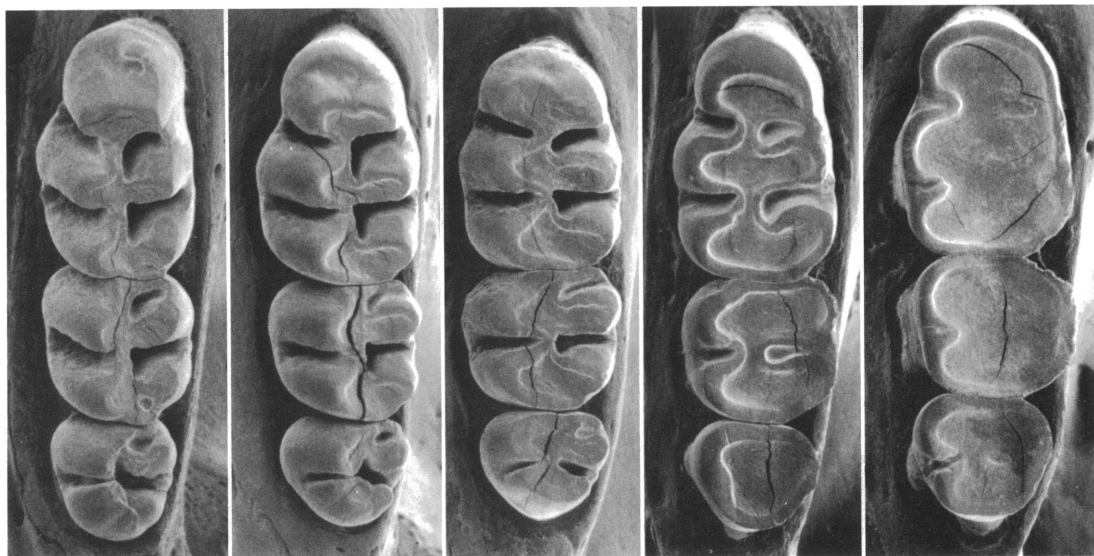


Fig. 4. Examples of molar toothwear classes from Finca Vuelta Larga (Venezuelan locality 69). From left, toothwear class 1 (AMNH 257333), toothwear class 2 (MHNLS 8137), toothwear class 3 (MHNLS 8155), toothwear class 4 (MHNLS 8140), toothwear class 5 (MHNLS 8161).

and Krzanowski, 1985), which appear to be nearly age-invariant in applications to muroid morphometric data (Voss and Marcus, in prep.). The unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973) was applied to Mahalanobis distance matrices to obtain the dendrograms in figures 26, 27, 29, and 30. Principal components were

extracted from the covariance matrix of log-transformed data following the recommendations of Jolicœur (1963), Morrison (1976), and Bookstein et al. (1985). The tabulated coefficients used to calculate principal component scores (table 17, fig. 28) are of eigenvectors scaled to unit length.

HISTORICAL SYNOPSIS

The early taxonomic history of *Zygodontomys* was reviewed by Tate (1932b) and the present account therefore abstracts or updates only those details necessary to understand current problems. Taxa from south of the Amazon that were formerly included in *Zygodontomys* (e.g., by Gyldenstolpe, 1932; Cabrera, 1961; Hershkovitz, 1962) but are now referred to *Akodon* or *Bolomys* (see Gardner and Patton, 1976; Reig, 1978, 1987; Maia and Langguth, 1981; Voss and Linzey, 1981) are only considered incidentally here.

Of the nominal species currently assigned to *Zygodontomys* (by Honacki et al., 1982), the oldest is *Oryzomys brevicauda*, described by Allen and Chapman in 1893 from specimens taken at "Prinkestown" (= Princes Town), Trinidad. Other species-group taxa

were described soon afterward based on collections from widely scattered localities: *O. microtinus* Thomas (1894) from "Surinam"; *Akodon punctulatus* Thomas (1894) from "Ecuador"; *O. cherriei* Allen (1895) from Boruca, in the Pacific littoral of eastern Costa Rica; and *Akodon frustrator* Allen and Chapman (1897) from Caura, Trinidad. In 1897 Allen erected *Zygodontomys*, designating *O. cherriei* as the type species, and also referred *O. brevicauda* to the new genus. Thomas (1898) referred his *O. microtinus* to *Zygodontomys*, commented on the diagnostic characters of the genus, and described a new species, *Z. brunneus*, from El Saibal, in the upper Magdalena valley of Colombia. Subsequently described forms and their type localities are: *Z. stellae* Thomas (1899) from

Maipures, in the Llanos of eastern Colombia; *Oryzomys sanctaemartae* Allen (1899) from Bonda, near the Caribbean coast of Colombia; *Z. brevicauda tobagi* Thomas (1900) from Richmond, on the island of Tobago; *Z. thomasi* Allen (1901) from Campo Alegre, in the eastern highlands of Venezuela; *Z. seorsus* Bangs (1901) from San Miguel Island, Panama; *Z. cherriei ventriosus* Goldman (1912) from Tabernilla, in central Panama; *Z. griseus* and *Z. fraterculus*, both named by Allen (1913) from different localities in the upper Río Magdalena valley of Colombia; *Orzyomys borroeroi* Hernandez-Camacho (1957) from Betulia, in the eastern Andes of Colombia; *Z. brevicauda soldadoensis* Goodwin (1965) from Soldado Rock, Trinidad; and *Z. reigi* Tranier (1976) from French Guiana.

Although the primary literature cited above recognizes 13 species, of which two are polytypic, no published summary of *Zygodontomys* taxonomy has followed this nominal arrangement. Gyldenstolpe (1932) and Ellerman (1941) regarded *brunneus* as a subspecies of *brevicauda*, a decision subsequently endorsed by Cabrera (1961) who recognized only two other mainland South American species, both polytypic. Hershkovitz (1962) combined all of the named forms currently referred to *Zygodontomys* into a single species, *Z. brevicauda*, with nine subspecies. Reig (1986), however, recognized four species from South America (and adjacent islands) and deemed the status of a fifth questionable.

Among these several classifications (table 1) there is little agreement. For example: *fraterculus* and *griseus*, both based on holotypes from the upper Magdalena valley of Colombia, are treated as subspecies of *Zygodontomys microtinus* and *Z. punctulatus*, respectively, by Cabrera (1961); as synonyms of *Z. brevicauda brunneus* by Hershkovitz (1962); and as distinct subspecies of *Z. punctulatus* by Reig (1986). Such disparate taxonomies have correspondingly different biological implications. While the many nominal species of the primary literature merely suggest extensive allopatric differentiation, Cabrera's species exhibit broad geographic overlap, implying reproductive isolation in areas of sympatry. By contrast, Hershkovitz's classification suggests reproductive continuity across the northern Neotropics from Costa Rica to

Ecuador and Surinam. Reig's species are all allopatric and their distributions appear to correspond with certain broadly defined zoogeographic regions. Unfortunately, neither Cabrera, Hershkovitz, nor Reig provided any discussions of characters or analyses of data to support their alternative opinions. Therefore, serious efforts to make biological sense of *Zygodontomys* species must be based, not on the literature, but on the direct evidence of similarity or difference provided by specimens.

Logically prior to any useful consideration of species problems, however, is the definition and diagnosis of the genus itself. Allen's (1897: 38) original description of *Zygodontomys* is succinct enough to quote in full:

Pelage full and soft, with the general appearance of *Sigmodon*. Skull characters in general much as in *Oryzomys*, but with a very different tooth-pattern. Teeth [the molars], in respect to relative size and general outline, as in *Oryzomys*, but the cross furrows [reentrant folds or flexi] between successive pairs of cusps are cut off by a longitudinal bar of enamel, yoking together the pairs of cusps on the median line of the tooth. Thus the anterior cone of m^1 is connected with the two succeeding pairs of cones by a median longitudinal ridge [the anterior and median mures], and the two pairs of cones in m^2 are similarly connected [by the median mure]. The same structure also characterizes the lower teeth.

Thomas (1898: 270) commented on this description as follows:

I use provisionally Dr. Allen's generic term *Zygodontomys*, as these short-tailed rats allied to *Oryzomys* seem to form a natural group, and there is a convenience in their having a special name. At the same time the dental character which he states to be peculiar to them, and on which he bases the name (the presence of a longitudinal ridge connecting the pairs of cusps), appears to occur in all *Oryzomys*, including the typical species *O. palustris* Harl. But *Zygodontomys* (as represented by *Z. brevicauda* and *Z. brunneus*) has a distinguishing character in the absence [Thomas's italics] of the transverse ridge [mesoloph or mesolophid] running outward from the longitudinal yoke between the pairs of cusps, and the consequent unusual simplicity of the molars. . . .

While Allen's original description and Thomas's emendation are clear enough, they are not adequately diagnostic because they fail to exclude many other Neotropical muroids that also have prominent mures/murids and lack well-developed mesolophs/mesolophids. Later, Thomas (1916) used different characters to define *Zygodontomys*, but by

TABLE 1
Species of *Zygodontomys* Recognized in the Primary Literature and in Subsequent Synopses

Primary Literature	Cabrera (1961) ^b	Hershkovitz (1962)	Reig (1986) ^c
<i>Z. borroeroi</i>	<i>Z. brevicauda brunneus</i>	<i>Z. brevicauda brevicau-</i>	<i>Z. brevicauda brevicauda</i> ^a
<i>Z. brevicauda brevicauda</i> ^a	<i>Z. microtinus fraterculus</i>	<i>da</i> ^{a,c}	<i>Z. b. tobagi</i>
<i>Z. b. soldadoensis</i>	<i>Z. m. microtinus</i>	<i>Z. b. brunneus</i> ^d	<i>Z. brunneus brunneus</i>
<i>Z. b. tobagi</i>	<i>Z. m. stellae</i>	<i>Z. b. cherriei</i>	<i>Z. b. sanctaemartae</i>
<i>Z. brunneus</i>	<i>Z. punctulatus griseus</i>	<i>Z. b. microtinus</i>	<i>Z. microtinus microtinus</i>
<i>Z. cherriei cherriei</i>	<i>Z. p. punctulatus</i>	<i>Z. b. punctulatus</i>	<i>Z. m. stellae</i>
<i>Z. c. ventriosus</i>	<i>Z. p. sanctaemartae</i>	<i>Z. b. sanctaemartae</i>	<i>Z. m. thomasi</i>
<i>Z. fraterculus</i>	<i>Z. p. thomasi</i>	<i>Z. b. seorsus</i>	<i>Z. punctulatus fraterculus</i>
<i>Z. griseus</i>		<i>Z. b. stellae</i>	<i>Z. p. griseus</i>
<i>Z. microtinus</i>		<i>Z. b. thomasi</i>	<i>Z. p. punctulatus</i>
<i>Z. punctulatus</i>		<i>Z. b. ventriosus</i>	<i>Z. reigi</i> ^f
<i>Z. reigi</i>			
<i>Z. sanctaemartae</i>			
<i>Z. seorsus</i>			
<i>Z. stellae</i>			
<i>Z. thomasi</i>			

^a Includes *Akodon frustrator*, a junior synonym based on immature specimens (Tate, 1932b).

^b Treated only mainland South American taxa.

^c *Z. b. tobagi* regarded as a synonym.

^d *Z. fraterculus* and *Z. griseus* regarded as synonyms.

^e Treated only South American and adjacent island forms.

^f Status deemed questionable.

then the genus had been expanded to embrace *Akodon*-like taxa that occur south of the Amazon: *Mus lasiurus* Lund and *Z. tapirapoanus* Allen (see Tate, 1932b). Although a consensus has emerged in recent years to exclude these (and other) southern taxa from *Zygodontomys* on the basis of their divergent karyotypic, dental, and reproductive attributes (Gardner and Patton, 1976; Maia and Langguth, 1981; Voss and Linzey, 1981; Reig, 1987), no corresponding refinement in the morphological characterization of *Zygodontomys* has been formalized.

The relationships of *Zygodontomys* to other Neotropical muroid genera have also been a source of confusion. The first known species were described as *Oryzomys* (see above), and both Thomas (1898) and Tate (1932b) appeared to endorse the notion that these genera are closely related. Thomas (1916) and Ellerman (1941), however, commented on the difficulty of distinguishing *Zygodontomys* from *Akodon*, and Vorontsov (1959) may have been influenced by their opinions when he referred *Zygodontomys* to the tribe Akodontini. Subsequently, Hershkovitz (1962) allied *Zygodontomys* with *Calomys* and other

members of the phyllotine group. While these conflicting perceptions of similarity were all based on a limited set of characters of the skin, skull, and dentition, new information from other organ systems has not provided compelling or consistent evidence either. Hooper and Musser (1964) noted similarities among the phalli of *Zygodontomys brevicauda*, *Oryzomys*, *Akodon*, and *Calomys*; in their phylogenetic diagram (1964: fig. 8b), *Zygodontomys* occupies an unresolved node near the base of the "South American Cricetine" radiation. Gardner and Patton (1976: 37) concluded from their comparisons of standard (unbanded) karyotypes that "... *Zygodontomys* and *Akodon* must have shared a common ancestor subsequent to the divergence of [the akodont] line from somewhere within the oryzomyine complex"; these authors did not, however, identify any derived karyotypic characters shared by *Zygodontomys* and *Akodon*, and the diploid counts of 84 to 88 chromosomes that they reported for *Zygodontomys* are much higher than those of any known akodont (see Reig, 1987). Carleton (1973) and Voss and Linzey (1981) reported primitive morphologies of the stom-

ach and male accessory glands, respectively, that contribute no information concerning relationships. The apparently equivocal phylogenetic position of *Zygodontomys* reflected in this literature led Reig (1980, 1984, 1986) to consider the genus incertae sedis within the subfamily Sigmodontinae, eschewing assignment to any tribal-level group.

In summary, there is little published basis for confident inference regarding any aspect of the systematic biology of *Zygodontomys*. If the genus and the species it contains are to be employed meaningfully in biological research, the historically troublesome issues identified above require critical attention.

THE GENUS

Zygodontomys J. A. Allen

Zygodontomys J. A. Allen, 1897: 38.

TYPE SPECIES: *Oryzomys cherriei* Allen (1895), based on an adult male specimen in the American Museum of Natural History consisting of a separately cataloged skin (AMNH 11297) and a skull with mandibles (AMNH 9557), collected by G. K. Cherrie on 10 December 1891 at Boruca, Provincia Puntarenas, Costa Rica; the upper left third molar is missing but the specimen is otherwise intact.

DISTRIBUTION: In unforested landscapes below 1500 m elevation from the Pacific littoral and foothills of eastern Costa Rica through Panama, Colombia, Venezuela, Guyana, Surinam, French Guiana, and Brazil north of the Amazon (see figs. 1 and 2). *Zygodontomys* also occurs on adjacent continental-shelf islands (Isla Cébaco, the Pearl Islands, Isla Margarita, Trinidad, and Tobago) where it may occupy forest as well as non-forest habitats. *Zygodontomys* is known from skeletal material found in caves on Aruba (Hooijer, 1967) but is not a member of the extant fauna of that island.

DIAGNOSIS: Rodents belonging to the muroid subfamily Sigmodontinae (sensu Carleton and Musser, 1984) with grizzled-brownish dorsal pelage; tail bicolored and much shorter than head-and-body; short mystacial vibrissae; small hindfeet with digits II–IV much longer than I and V; eight mammae in inguinal, abdominal, postaxial, and pectoral pairs; convergent, beaded interorbital margins of skull; incisive foramina long and widest behind premaxillary/maxillary suture; palate long and pitted posterolaterally; alisphenoid strut absent (buccinator-masticatory foramen and foramen ovale confluent);

upper incisors ungrooved and opisthodont; anterocone(id) of M1/m1 undivided; labial and lingual molar cusps arranged in opposite pairs and connected by transverse lophs orthogonal to long axis of toothrow; mesolophs and mesolophids entirely absent; first upper molar with three roots, first lower molar with two; gall bladder absent; penis complex, with tridigitate baculum.

MORPHOLOGICAL DESCRIPTION: Pelage short, close, grizzled-brownish dorsally; washed ventrally with white, pale gray, or yellowish tones but the base of the ventral hairs always dark gray. Ears sparsely haired, not large. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present; mystacial vibrissae short, not extending posteriorly much beyond base of pinna when laid flat against cheek. Manus and pes covered dorsally with short, pale hairs; distinctly longer hairs form tufts at bases of claws. Manus with two carpal and three interdigital plantar pads; pes with two metatarsal and four interdigital pads; naked epidermis of plantar surface scaly between pads. Hindfoot small (about one-fifth of head-and-body length), with middle digits much longer than outer digits (claw of I extends about half the length of first phalange of II; claw of V extends only to first interphalangeal joint of IV). Tail short (about three-quarters the length of head-and-body), distinctly bicolored (dark above, pale below), sparsely haired, and without tuft or pencil of distinctly longer hairs at tip. Eight mammae in inguinal, abdominal, postaxial, and pectoral pairs.

Skull (Fig. 5A) unremarkable in dorsal view; rostrum neither very long nor very short; zygomatic notch of maxillary bone conspicuous on each side of rostrum, deeply excavated; interorbital region convergent, beaded; in-

terorbital bead continuous with prominent ridge marking origin of temporalis muscle on dorsolateral aspect of braincase in mature specimens; zygomatic arches convergent (widest across squamosal roots) or bowed laterally (widest across jugals); braincase small in relation to facial skeleton in mature specimens, oblong, not inflated. Zygomatic plate broad, varying in shape within populations but anterior edge always straight or concave rostrally (never sloping posteriorly from base). Incisive foramina long, usually extending posteriorly to or between molar alveoli; widest behind maxillary/premaxillary suture. Palatal bridge broad and smooth, without conspicuous ridges, deep furrows, or large spinelike median posterior process; with one or more usually prominent posterolateral pits. Mesopterygoid fossa usually with rounded anterior margin, not extending rostrally between third molars in adults; bony roof of fossa complete or perforated by sphenopalatine vacuities. Parapterygoid fossae narrow and not deeply excavated. Large stapedial foramen in petrotympanic fissure present but other osteological traces of carotid circulation variable. Vertical strut of alisphenoid absent (buccinator-masticatory foramen and foramen ovale confluent). Auditory bullae small and flask-shaped. Subsquamosal fenestra usually present but often small; absent from occasional specimens in many samples.

Mandible with well-developed, falciform coronoid process; capsular process of lower incisor alveolus usually below (if not, then slightly posterior to) base of coronoid process; tip of angular process below or produced posteriorly beyond articular condyle. Basihyoid without entoglossal process.

Upper incisors smooth (never grooved), narrow, and opisthodont; the enamel band bright yellow-orange. Lingual and labial molar cusps arranged in strictly opposite pairs (not alternating) on both upper and lower teeth. Upper molar rows parallel; anterocone of M1 undivided by anteromedian flexus (except as rare variant in a few samples); anteroloph absent as a discrete structure on M1, well developed on M2 and (usually) M3; mesoloph absent; posteroloph small and usually obliterated with slight wear on all upper teeth; M3 small, about $\frac{3}{4}$ to $\frac{1}{2}$ size of M2 (varying within populations); upper teeth all with three

roots each. Anteroconid of m1 undivided by anteromedian flexid; anterolophid absent on all lower teeth; anterolabial cingulum present on unworn m2 and m3; mesolophid absent on all lower teeth; well-developed posterolophid present on m1 and m2, absent from m3; m1 with two roots, m2 with three roots, m3 with two or three roots.

Axial skeletal elements exhibiting little variation in number, with modal counts of 12 ribs, 19 thoracicolumbar vertebrae, four sacral vertebrae, and 24 to 26 caudal vertebrae in all available population samples. First rib articulates with transverse processes of seventh cervical and first thoracic vertebrae. Second thoracic vertebra with hypertrophied neural spine. Entepicondylar foramen of humerus absent.

Stomach unilocular and hemiglandular (Carleton, 1973: fig. 2). Gall bladder absent. Male accessory glands consist of one pair each of preputial, bulbourethral, anterior and dorsal prostate, ampullary, and vesicular glands, and two pairs of ventral prostrate glands (Voss and Linzey, 1981). Glans penis complex, with tridigitate bacular cartilage and deep terminal crater containing three bacular mounds, one dorsal papilla, and a bifurcate urethral flap (Hooper and Musser, 1964: fig. 5).

CONTENTS: Sixteen nominal species-group taxa are referred to the genus as follows in chronological order of their descriptions: *Oryzomys brevicauda* J. A. Allen and Chapman, *O. microtinus* Thomas, *O. cherriei* J. A. Allen, *Akodon frustrator* J. A. Allen and Chapman, *Zygodontomys brunneus* Thomas, *Z. stellae* Thomas, *O. sanctaemartae* J. A. Allen, *Z. brevicauda tobagi* Thomas, *Z. thomasi* J. A. Allen, *Z. seorsus* Bangs, *Z. cherriei ventriosos* Goldman, *Z. griseus* J. A. Allen, *Z. fraterculus* J. A. Allen, *O. borroeroi* Hernández-Camacho, *Z. brevicauda soldadonesis* Goodwin, and *Z. reigi* Tranier.

The nominal species *Akodon punctulatus* Thomas does not belong in *Zygodontomys*; its proper assignment to genus is the topic of another report (Voss, in press).

COMPARISONS WITH *BOLOMYS*

The species originally described as *Mus lasiurus* by Lund (1838) was until recently included in *Zygodontomys* (Cabrera, 1961;

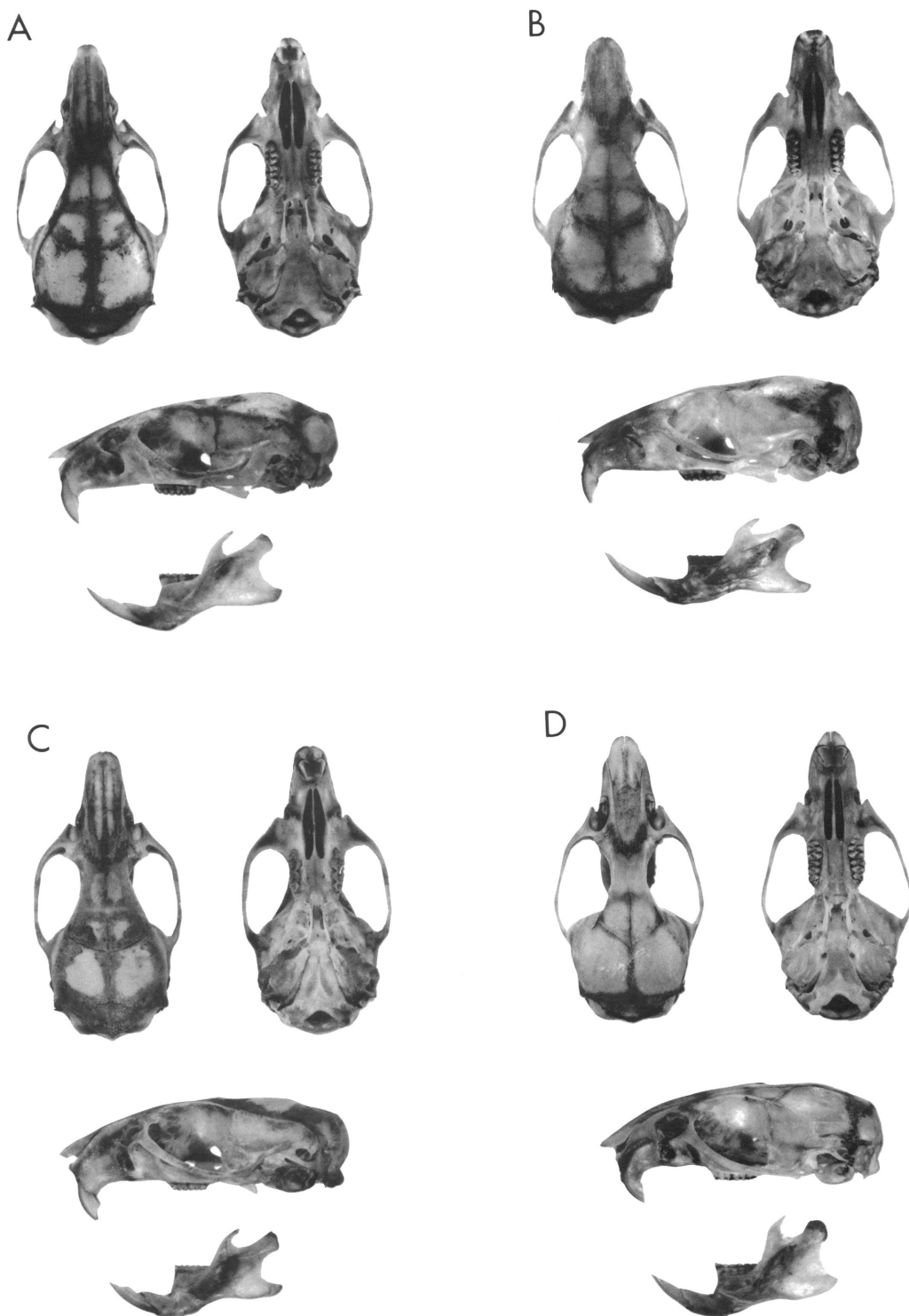


Fig. 5. Skulls and mandibles of four muroid species. A, *Zygodontomys brevicauda* (USNM 547978); B, *Bolomys lasiurus* (AMNH 211835); C, *Calomys callosus* (AMNH 260744); D, *Pseudoryzomys simplex* (UCM 16488).

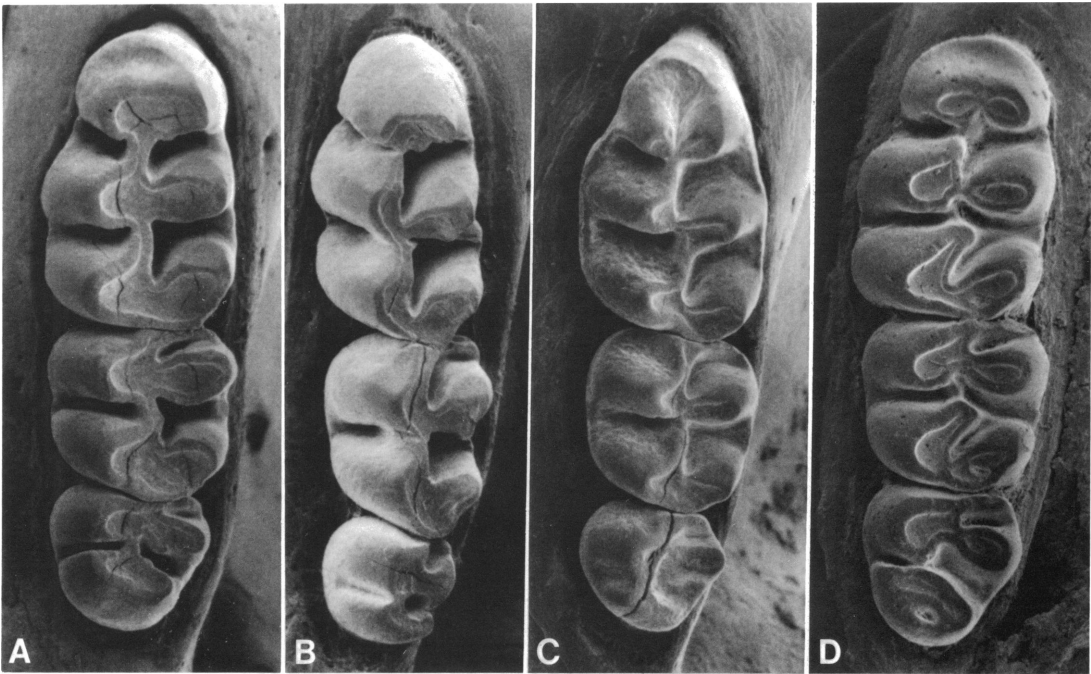


Fig. 6. Left upper molars of four muroid species. A, *Zygodontomys brevicauda* (AMNH 173971); B, *Bolomys lasiurus* (AMNH 214541); C, *Calomys callosus* (AMNH 246851); D, *Pseudoryzomys simplex* (UCM 17060).

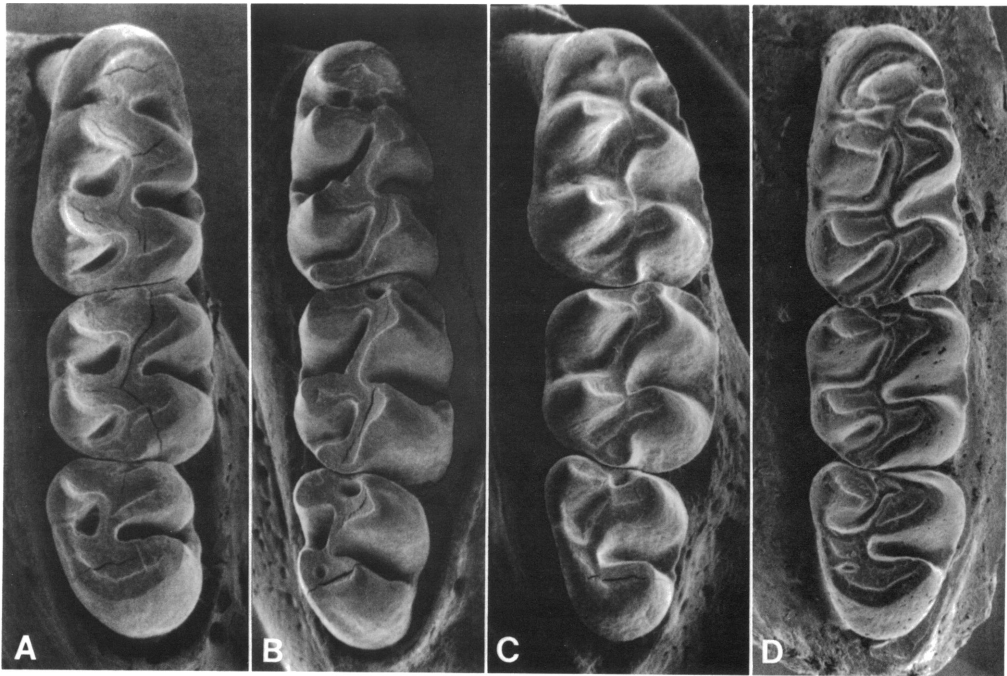


Fig. 7. Right lower molars of four muroid species. Specimens are the same as those in figure 6.

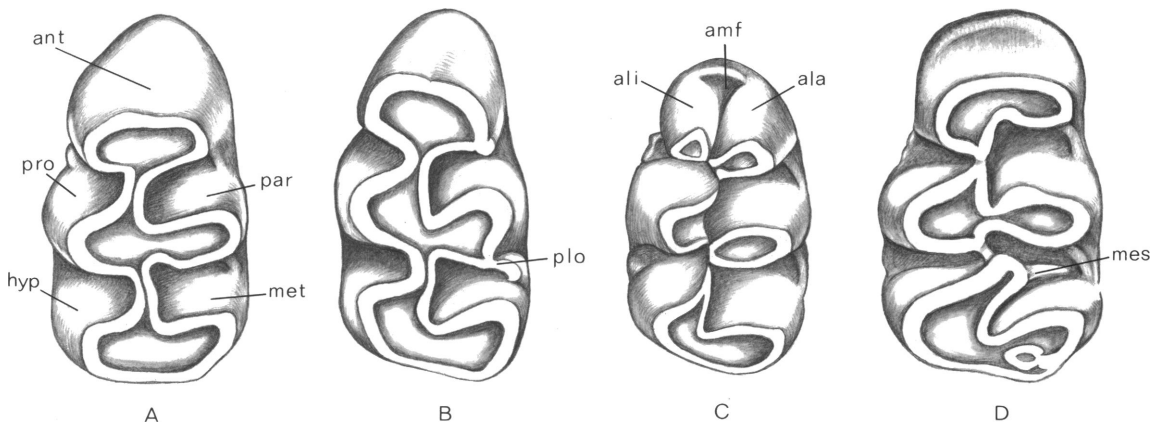


Fig. 8. First upper molars. A, *Zygodontomys brevicauda* (AMNH 184776); B, *Bolomys lasiurus* (AMNH 210151); C, *Calomys callosus* (AMNH 260652); D, *Pseudoryzomys simplex* (UCM 15757). *ala*, anterolabial conule; *ali*, anterolingual conule; *amf*, anteromedian flexus; *ant*, anterocone; *hyp*, hypocone; *mes*, mesoloph; *met*, metacone; *par*, paracone; *plo*, paralophule; *pro*, protocone.

Hershkovitz, 1962) but is now regarded (e.g., by Reig, 1978, 1987) as a member of the akodont genus *Bolomys*.¹ *Bolomys lasiurus* is a common inhabitant of nonforest lowland vegetation south of the Amazon, from Brazil through Paraguay and northern Argentina to eastern Bolivia (map in Macedo and Mares, 1987). The species may yet be found to occur sympatrically with *Zygodontomys* in coastal savannas of the Brazilian state of Amapá (north of the Amazon delta), but no collections of either taxon are currently known from that region. Comparisons between *B. lasiurus* and *Zygodontomys* serve to clarify the discriminatory value of characters cited in the preceding generic diagnosis, but other species

of *Bolomys* that have never been confused with *Zygodontomys* (e.g., *B. amoenus* and *B. lactens*) are not considered here.

Bolomys lasiurus and *Zygodontomys* are similar in external appearance: they are grizzled-brownish rats with short mystacial vibrissae; short, bicolored tails; small hindfeet with digits II–IV much longer than I and V; and eight mammae. Although subtle differences exist even in these external characters, the two taxa are best distinguished by comparisons of teeth, skulls, and viscera.

The molar dentition of *Zygodontomys* (figs. 6A, 7A, 8A) is distinctive in the compact arrangement of labial and lingual cusps in opposite pairs, and in the absence of accessory enamel structures that often complicate the occlusal morphology of other Neotropical Sigmodontinae. By contrast, the principal molar cusps of *Bolomys lasiurus* (figs. 6B, 7B, 8B) alternate in their anteroposterior placement, and small paralophules² project pos-

¹ I follow Cabrera (1961) and Hershkovitz (1962) in treating all of the following as conspecific: *Akodon fuscinus* Thomas, *A. linguarum* Thomas, *Mus lasiurus* Lund, *Zygodontomys pixuna* Moojen, and *Z. tapirapoanus* J. A. Allen. Of these, the oldest name is Lund's. Reig (1987) regarded *linguarum* ("probably including" *tapirapoanus*) as a species distinct from *lasiurus* (including *fuscinus* and *pixuna*), an arrangement also followed by Anderson and Olds (1989), but no diagnosis has yet been provided for either taxon. While some morphometric analyses (e.g., Macedo and Mares, 1987) suggest the presence of significant geographic variation among samples of *lasiurus* (sensu Cabrera-Hershkovitz), it is convenient to use only one binomial in reference to them pending a critical taxonomic revision of the group. Finally, the perception that *lasiurus* and its allies do not belong in the genus *Zygodontomys* should be credited to Tate (1939) whose early insight was ignored by all later workers.

² Hooper (1957) identified these small structures adnate to the posterolabial aspect of the paracone as vestigial (or nascent) mesolophes, but Hershkovitz (1962) argued that both paralophule and mesoloph can occur on the same tooth and are therefore not homologous (i.e., part of the same transformation series as shown in Hooper's fig. 1). Hershkovitz cited no example, but both structures are clearly present and discrete in the unworn dentitions of some akodonts (e.g., *Abrothrix sanborni*); in others (e.g., *Akodon* sensu stricto), both structures seem to be present but indistinguishably coalesced. In *Bolomys lasiurus*, the mesoloph appears to be absent.

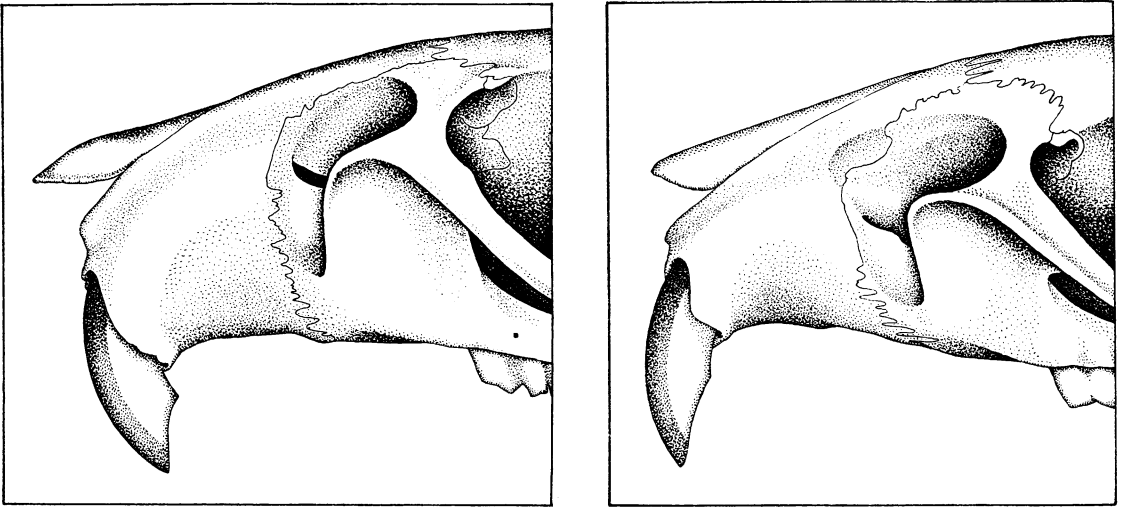


Fig. 9. Lateral view of rostrum. **Left**, *Zygodontomys brevicauda* (MHNLS 8154); **right**, *Bolomys lasiurus* (AMNH 210155).

terolabially from the paracones of unworn first and second upper teeth (fig. 8B, plo). Another character, cited by Voss and Linzey (1981) to distinguish the molar occlusal pattern of *Zygodontomys* from that of *B. lasiurus*, is the colinearity of anterior and median mures on the first upper molars of the former, but this trait is not exhibited by all *Zygodontomys* species: *Z. brunneus* of the intermontane valleys of Colombia has oblique mures that are not colinear on M1 (see below).

The first upper molar of *Bolomys lasiurus* has four roots, one anterior (above the anterocone), one posterior (above the metacone), one lingual (above the protocone and hypocone), and one labial (above the paracone). The latter, labial root (occasionally divided to form two smaller rootlets) is not externally visible in young individuals but becomes increasingly exposed to lateral view with age. The first upper molars of *Zygodontomys* species have only three roots apiece: one anterior, one posterior, and one lingual; a labial root is never present. Lower first molars also differ in root number between the two taxa. In *B. lasiurus* this tooth always has at least three roots, one anterior (below the anteroconid), one posterior (below the entoconid and hypoconid), and one labial (below the protoconid); another smaller, lingual root is sometimes present below the metaconid. The first lower molar of *Zygodonto-*

mys has only one anterior root and one posterior root.

The morphology of the upper incisors and rostrum differs dramatically between *Zygodontomys* and *Bolomys lasiurus*. The rostrum of *Zygodontomys* (fig. 9, left) is deep throughout its length, from zygomatic root to nasal orifice; the nasal bones are long, projecting anteriorly well beyond the premaxillae; and the incisors are strongly opisthodont (posteroventrally recurved). In *B. lasiurus* (fig. 9, right), however, the rostrum tapers conspicuously from zygomatic root to nasal orifice; the nasal bones are short and do not project anteriorly much beyond the premaxillae; and the procumbent incisors are nearly or quite orthodont.

Both *Zygodontomys* and *Bolomys lasiurus* have long incisive foramina that usually extend posteriorly to or between the first molars. In *Zygodontomys* (fig. 10, left) the foramina are widest behind the premaxillary/maxillary suture and taper anteriorly from this convex middle part. In *B. lasiurus* (fig. 10, right), however, the foramina are widest anteriorly, at or near the premaxillary/maxillary suture, and taper only slightly posteriorly so that the lateral edges of the foramina appear almost parallel for much of their extent.

The morphology of the posterior bony palate in relation to the molar rows and to paired clusters of small foramina also distinguishes

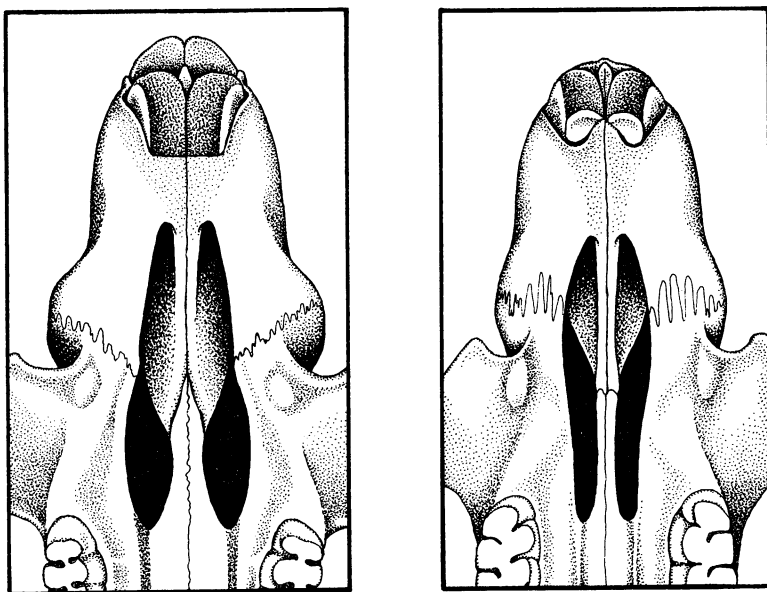


Fig. 10. Incisive foramina in diastemal plate. **Left**, *Zygodontomys brevicauda* (MHNLS 8156); **right**, *Bolomys lasiurus* (AMNH 210188).

Zygodontomys from *Bolomys lasiurus* (fig. 11). In adult specimens of *Zygodontomys* (the palatal morphology of very young animals is distorted by the presence of an adult-size molar dentition in an immature facial skeleton) the palate is "long" in the sense defined by Hershkovitz (1962): the mesopterygoid fossa does not extend anteriorly to or between the third molars, and the bony palate is therefore produced behind those teeth. The anterior limit of the fossa usually has the shape of a rounded or pointed arch in *Zygodontomys*, but a minute median palatal process is present as an uncommon variant in some samples. Between the mesopterygoid fossa and the third molars on both sides are one to several distinct pits (if several, then these pits are usually clustered and may be recessed together in a shallow fossa). These posterolateral palatal pits are always present and conspicuous in *Zygodontomys* (fig. 11, top, ppp) despite their variation in number and configuration from individual to individual. In *B. lasiurus* the bony palate is "short" because the mesopterygoid fossa extends to or between the third molars; the anterior limit of the fossa is square or, commonly, biconcave when a small posterior palatal process is present. There are no distinct posterolateral pal-

atal pits in *B. lasiurus* (fig. 11, middle) although tiny foramina are sometimes present in the palatine bones lateral to the mesopterygoid fossa.

The buccinator-masticatory foramen and the accessory oval foramen are separated by a vertical pillar or strut of the alisphenoid bone in many muroid rodents. In *Zygodontomys*, however, the latter structure is absent and the two foramina are therefore confluent (fig. 12, left). A few specimens (about 3% of 701 individuals scored for this trait) exhibit a slender, vertical splint of bone behind the trough or groove that marks the passage of the buccinator and masticatory nerves along the outside of the braincase; such fragile ossifications usually occur on just one side of the skull. By contrast, a robust alisphenoid strut always separates the buccinator-masticatory foramen and the accessory oval foramen in *Bolomys lasiurus* (fig. 12, right).

The root of the rodent lower incisor is often contained in a bony tubercle, the capsular process, that projects from the lateral surface of the mandible. In *Zygodontomys* (fig. 13, top), the capsular process is situated at or near the base of the coronoid process, whereas the capsular process of *B. lasiurus* is more posteriorly located, between the coronoid and

articular processes (fig. 13, bottom). Mandibles of the two taxa also differ strikingly in shape: the lower incisor of *Zygodontomys* is stout and strongly recurved, the angle of the jaw is broad and blunt, and the dentary is tall (from coronoid to angle) in proportion to its length. By contrast, the lower incisor of *Bolomys* is slender and procumbent, the angular process is more attenuate, and the dentary is proportionately shallower.

In *Bolomys lasiurus* (and many other Neotropical muroids), a large, saccular gall bladder is concealed in the deep fissure that divides the median or cystic lobe of the liver into left and right halves. *Zygodontomys* lacks a gall bladder.

COMPARISONS WITH *CALOMYS*

Most species of *Calomys* occur in unforested highland habitats of the central Andes or in the unforested lowlands of southern Brazil, Paraguay, Uruguay, northern Argentina, and eastern Bolivia (map in Hershkovitz, 1962: fig. 28). *Calomys hummelincki*, however, has a disjunct range and occurs sympatrically with *Zygodontomys* in the Llanos and other unforested lowland habitats of Venezuela and Colombia (see Handley, 1976; and Petter and Baud, 1981, who report a Colombian specimen as *C. laucha*). Hershkovitz (1962) placed *Zygodontomys* in the "*Calomys*" section of his phyllotine group, citing resemblances between *C. callosus* and *Zygodontomys* as evidence of a close relationship. All species of *Calomys* resemble *Zygodontomys* in possessing long incisive foramina (fig. 5C), long palates with prominent posterolateral pits (fig. 11, bottom panel), and in the complete absence of mesolophids (figs. 6C, 7C, 8C). In addition, *C. callosus* and *C. venustus*³ resemble *Zygodontomys* in size (other species of *Calomys* are substantially smaller); in their short, grizzled-brownish dorsal pelage and dull underparts (*C. lepidus* has a deep, soft, marbled pelage, and most

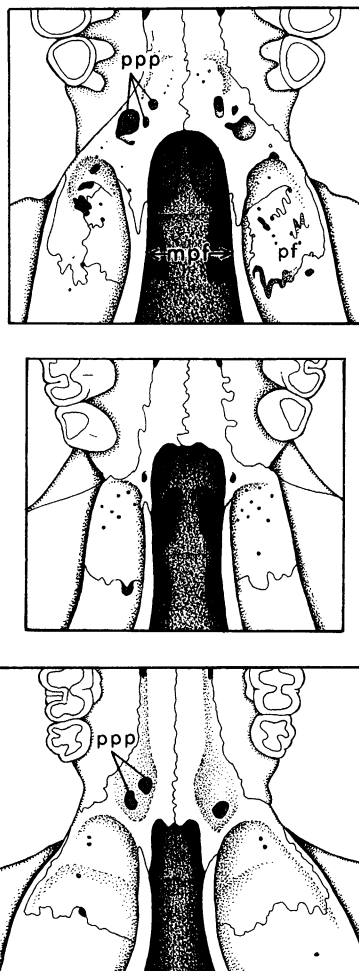


Fig. 11. Posterior palate and pterygoid region of *Zygodontomys brevicauda* (top, AMNH 257323), *Bolomys lasiurus* (middle, AMNH 210153), and *Calomys callosus* (bottom, AMNH 260651). **mpf**, mesopterygoid fossa; **pf**, pterygoid fossa; **ppp**, posterior palatal pits.

specimens of *C. hummelincki* have bright buff-colored upperparts that contrast with whitish venters); in relative tail length (*C. murillus* and *C. musculus* have tails as long or longer than heads-and-bodies); in their beaded, convergent supraorbital margins (most other species of *Calomys* lack sharp supraorbital beads and some have parallel-sided interorbital morphologies); and in the absence of an alisphenoid strut (*C. laucha* and *C. tener* usually exhibit alisphenoid struts).

³ *Calomys venustus* was regarded by Hershkovitz (1962) as a subjective junior synonym of *C. callosus* but is considered by Olds (1988) to be a distinct species. I follow Olds (1988) throughout this discussion, treating the following as full species: *C. bimaculatus*, *C. callosus*, *C. hummelincki*, *C. laucha*, *C. lepidus*, *C. murillus*, *C. musculus*, *C. sorellus*, *C. tener*, and *C. venustus*.

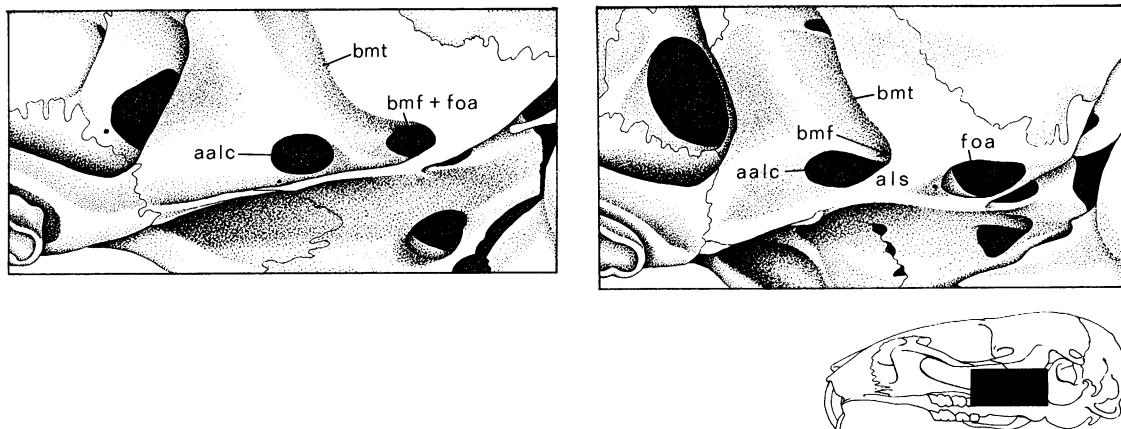


Fig. 12. Alisphenoid region. **Left**, *Zygodontomys brevicauda* (MHNLS 8133); **right**, *Bolomys lasiurus* (AMNH 210158). **aalc**, anterior opening of alisphenoid canal; **bmf**, buccinator-masticatory foramen; **bmt**, buccinator-masticatory trough; **foa**, foramen ovale accessorius.

All species of *Calomys* resemble one another, however, and differ from *Zygodontomys* in the characters described below.

The anterocone of the first upper molar in *Calomys* is always divided by a prominent fold (the anteromedian flexus) into anterolingual and anterolabial conules of which the latter is consistently larger (figs. 6C, 8C); the anteroconid of the lower first molar is likewise divided, by the anteromedian flexid, into small lingual and labial conulids (fig. 7C).

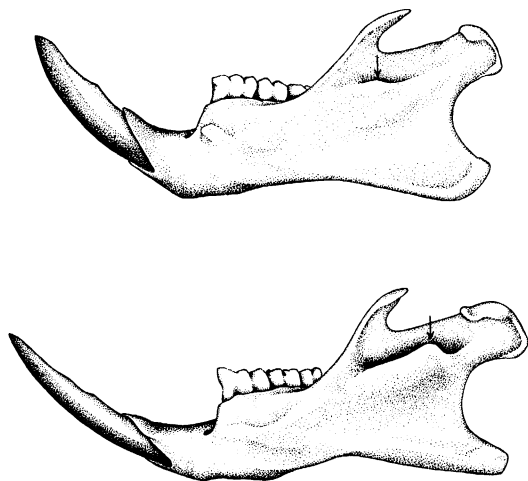


Fig. 13. Lateral view of mandible. **Top**, *Zygodontomys brevicauda* (MHNLS 8147); **bottom**, *Bolomys lasiurus* (AMNH 210151). Vertical arrows mark the capsular process of the lower incisor alveolus.

Both the anterocone and the anteroconid of *Zygodontomys*, by contrast, are entire and undivided (figs. 6A, 7A, 8A). Another point of molar difference is the conspicuous alternation of labial and lingual cusps along the anteroposterior axis of the toothrow in *Calomys*. Consequently, the paracone is not connected directly to the protocone, but instead attaches to the median mure. In *Zygodontomys*, labial and lingual cusps are arranged in opposite pairs and the paracone is connected directly with the protocone.

The first upper molar of *Calomys* has four roots, one anterior, one posterior, one lingual, and one labial, with the same anatomical relations to the principal cusps as described above for *Bolomys lasiurus*; the labial root is the smallest but it is always externally visible in adult specimens. The first lower molar of *Calomys* also has at least three roots, like *B. lasiurus*, and a fourth (lingual) root is often present as well. *Zygodontomys* has three first upper molar roots and two first lower molar roots as described earlier.

Behind the molar rows and to either side of the mesopterygoid fossa are the parapterygoid fossae within which the internal pterygoid muscles originate. The parapterygoid fossae are very large in *Calomys*; their lateral margins are conspicuously expanded and the mesopterygoid fossa is squeezed to a narrow slit between their medial limits (fig. 11, bottom). By contrast, the parapterygoid fossae of *Zygodontomys* are narrow and the meso-

pterygoid fossa between them is correspondingly wide (fig. 11, top).

In *Calomys*, a large gall bladder is situated between the right and left halves of the cystic lobe of the liver. *Zygodontomys* lacks a gall bladder.

Additional characters provide less satisfactory comparisons but contribute to the impression that each genus is a distinct, natural group.

Most species of *Calomys* (including *C. callosus* and *C. venustus*) have patches of whitish or buffy fur behind the ears, but such postauricular spots may be indistinct or absent in occasional specimens from large population samples. No species of *Zygodontomys* exhibits postauricular spots.

Some species of *Calomys* usually have eight mammae like *Zygodontomys*, but mammae vary in number within and among *Calomys* species; in *C. callosus* mammae counts range from 8 to 12, in *C. venustus* from 10 to 14 (Olds, 1988).

An anteromedian style (a distinct cusplet arising from the front of the anterocone on the first upper molar) is present at frequencies of 8 to 100 percent of specimens in different species of *Calomys*; across species, the mean frequency of occurrence of the anteromedian style is about 45 percent, based on specimens counted by Olds (1988). No such structure occurs in *Zygodontomys*.

COMPARISONS WITH PSEUDORYZOMYS

The genus *Pseudoryzomys* contains one species, *P. simplex* (see Voss and Myers, 1991), that ranges south of the Amazon in unforested tropical and subtropical lowlands from eastern Brazil and northern Argentina through Paraguay to eastern Bolivia. *Pseudoryzomys* resembles *Zygodontomys* in a number of external and cranial characters, some of which were noted by Hershkovitz (1962): both taxa have grizzled-brownish dorsal pelage; short mystacial vibrissae; sparsely haired, bicolored tails; hindfeet with digits II, III, and IV much longer than I and V; eight mammae in inguinal, abdominal, postaxial, and pectoral pairs; convergent, beaded supraorbital margins; long incisive foramina; long palates with prominent pos-

terolateral pits; and narrow parapterygoid fossae (see fig. 5D for cranial views of *P. simplex*). Resemblances are most striking, however, in the occlusal morphology of the upper molars: the principal cusps of both *Pseudoryzomys* and *Zygodontomys* are arranged in opposite labial-lingual pairs, and the opposing cusps of each pair are connected directly across the midline of the tooth by transverse lophs, not (as in *Bolomys* and *Calomys*) linked by separate attachments to the median mure (fig. 8 A, D). Despite such similarities, however, differences between *Pseudoryzomys* and *Zygodontomys* are numerous.

The hindfoot of *Pseudoryzomys* is narrow and long, averaging about one-fourth of the length of the head and body. The plantar surface of the heel is smooth, but the skin between the plantar pads and at the bases of the toes is densely set with small tubercules; small webs of skin extend about halfway between the first phalanges of digits II, III, and IV. The hindfoot of *Zygodontomys*, by contrast, is broader and proportionately shorter, averaging about one-fifth of head-and-body length; the plantar epithelium is not so conspicuously tubercular, and interdigital webbing, when present, is inconspicuous.

The tail is distinctly longer in *Pseudoryzomys*, averaging about as long as the head and body; in *Zygodontomys* the tail averages about three-fourths of head-and-body length.

The alisphenoid strut that separates the buccinator-masticatory and accessory oval foramina in *Bolomys lasiurus* and in some species of *Calomys* may be present or absent in *Pseudoryzomys*; it is absent in *Zygodontomys*.

The stapedial foramen, located in the petrotympanic fissure on the posteromedial aspect of the auditory bulla, transmits the stapedial artery to the middle ear cavity. In *Zygodontomys*, the stapedial artery and foramen are large; the artery passes entirely through the bulla, enters the braincase, and courses forward with or without major divisions to enter the orbit, whence it supplies the facial (ophthalmic and internal maxillary) circulation. *Pseudoryzomys*, however, exhibits an alternative circulatory morphology in which the facial circulation is not supplied by the stapedial artery but instead by a branch of the internal carotid that arises on the floor

of the braincase and passes obliquely across the roof of the parapterygoid fossa to enter the orbit through the anterior alar fissure; the stapedial foramen is very small and may be difficult to see at all. The carotid morphology of *Zygodontomys* corresponds to patterns 1 and 2 of Voss (1988), whereas that of *Pseudoryzomys* corresponds to pattern 3 and is also identical with the morphology described by Carleton and Musser (1989) for *Oryzomys palustris*.

A mesoloph is invariably present on the first and second upper molars of *Pseudoryzomys* (fig. 8D, mes). However, unlike *Oryzomys* and other pentalophodont genera in which this crest is prominent and extends from the median mure all the way to the labial cingulum, the mesoloph of *Pseudoryzomys* is small and never fuses with a labial mesostyle. *Zygodontomys* (fig. 8A) lacks any trace of a mesoloph. The first upper molars of the two genera also differ by the presence, in *Pseudoryzomys*, of a fourth (labial) root above the paracone; as described above, this tooth is three-rooted in *Zygodontomys*.

The principal labial and lingual cusps of the lower molars (fig. 7D) alternate slightly along the anteroposterior axis of the toothrow in *Pseudoryzomys*, by contrast with the opposite arrangement in *Zygodontomys* (fig. 7A). The first lower molar of *Pseudoryzomys* is, additionally, four-rooted; a labial root (below the protoconid) and a lingual root (below the metaconid) are present together with the anterior and posterior roots that alone anchor this tooth in *Zygodontomys*.

PHYLOGENETIC RELATIONSHIPS

Relationships among Neotropical muroid genera are usually discussed in terms of membership in groups that, following Vorontsov (1959), have been ranked as tribes in the Linnaean system. The most recent comprehensive classification of Neotropical muroids (Reig, 1984) places *Bolomys* in the tribe Akodontini, and *Calomys* and *Pseudoryzomys* in the tribe Phyllotini, but leaves *Zygodontomys* unclassified as Sigmodontinae incertae sedis. Subsequently, Olds and Anderson (1989) removed *Pseudoryzomys* from the Phyllotini; since they did not assign the genus to another tribal group, it too is currently

incertae sedis in the subfamily. Unless accompanied by substantive analyses of character data, however, such taxonomic arrangements are of uninterpretable biological significance. While diagnoses have recently been proposed for the Akodontini (Reig, 1987) and for the Phyllotini (Olds and Anderson, 1989), no compelling evidence that either taxon is monophyletic has been reported, and the empirical basis for recognizing most other tribes of Neotropical muroids is still less satisfactory. Therefore, the existing suprageneric classification does not provide an adequate framework for meaningful phylogenetic discussions.

The taxa considered earlier—*Bolomys*, *Calomys*, and *Pseudoryzomys*—are those with which *Zygodontomys* has often been compared or confused in the literature, and there are no other Neotropical muroids that *Zygodontomys* more closely resembles. Hence, the morphological attributes described in the preceding comparative accounts (table 2) provide an empirical basis for preliminary efforts to identify sister-group relationships.

Not all of the comparisons that distinguish *Zygodontomys* from *Bolomys*, *Calomys*, and *Pseudoryzomys* are suitable for cladistic analysis. The partially webbed hindfeet and carotid circulation of *Pseudoryzomys* are autapomorphic (among these four genera), as are the expanded parapterygoid fossae and bifurcated anterocones/anteroconids of *Calomys*. Another basis for comparison, relative tail length, is a proportion so variable among Neotropical muroids that no confident judgment can be made about the primitive condition. Finally, the occurrence of posterolateral palatal pits and the length of the palate seem unlikely to be independent in their anatomical transformations and are best regarded as a single character. Consequently, only eight characters can be formalized to serve as a basis for phylogenetic inference among these four taxa (below, and table 3). The state designated (0) is presumed primitive for each following the polarities suggested by Hershkovitz (1962), Reig (1977), Carleton (1980), and Carleton and Musser (1984).

Character 1. Palatal morphology:

- (0) palate short (not produced behind molar rows) and without conspicuous posterolateral pits;

TABLE 2
Morphological Character Variation Among Four Neotropical Muroid Taxa

Character	<i>Zygodontomys</i>	<i>Bolomys lasiurus</i>	<i>Calomys callosus</i>	<i>Pseudoryzomys simplex</i>
Digits of hindfoot:	free	free	free	webbed
Tail length:	<HBL	<HBL	<HBL	=HBL
Palate:	long	short	long	long
Posterolateral palatal pits:	present	absent	present	present
Parapterygoid fossae:	narrow	narrow	wide	narrow
Alisphenoid strut:	absent	present	absent	present/absent
Facial circulation:	stapedial	stapedial	stapedial	int. carotid
Anterocone/anteroconid:	entire	entire	divided	entire
Upper molar cusps:	opposite	alternate	alternate	opposite
Lower molar cusps:	opposite	alternate	alternate	alternate
Mesoloph:	absent	absent	absent	present
M1 roots:	three	four	four	four
m1 roots:	two	three or four	three or four	four
Gall bladder:	absent	present	present	absent ^a

^a Field dissection of a single specimen.

- (1) palate long (produced behind molar rows), with conspicuous posterolateral pits.

Character 2. Alisphenoid strut:

- (0) strut present, separating buccinator-masticatory and accessory oval foramina;
(1) strut present or absent (polymorphic);
(2) strut absent, buccinator-masticatory and accessory oval foramina confluent (derived from state 1).

Character 3. Upper molar cusps:

- (0) principal cusps of upper molars arranged in opposite labial-lingual pairs;
(1) principal cusps of upper molars alternating in anteroposterior position.

Character 4. Lower molar cusps:

- (0) principal cusps of lower molars arranged in opposite labial-lingual pairs;
(1) principal cusps of lower molars alternating in anteroposterior position.

Character 5. Mesoloph:

- (0) mesoloph small but present;
(1) mesoloph absent.

Character 6. First upper molar roots:

- (0) M1 with three roots (labial root absent);
(1) M1 with four roots (labial root present).

Character 7. First lower molar roots:

- (0) m1 with two roots (labial and lingual roots absent);
(1) m1 with three or four roots (labial root present, lingual root present or absent).

Character 8. Gall bladder:

- (0) present;
(1) absent.

An exhaustive search for the most parsimonious phylogenetic hypothesis supported by these characters (implemented by PAUP version 3.0; Swofford, 1989) discovered one tree of length 14 steps (fig. 14A) that identifies *Zygodontomys* as the sister group of a clade composed of *Bolomys*, *Calomys*, and *Pseudoryzomys*. Four other trees (fig. 14B–E) are only one step longer, however, and such a small difference in parsimony provides no

TABLE 3
Matrix of Character State Distributions for Phylogenetic Analysis

	Characters ^a							
	1	2	3	4	5	6	7	8
<i>Bolomys</i>	0	0	1	1	1	1	1	0
<i>Calomys</i>	1	2	1	1	1	1	1	0
<i>Pseudoryzomys</i>	1	1	0	1	0	1	1	1
<i>Zygodontomys</i>	1	2	0	0	1	0	0	1

^a As defined in the text.

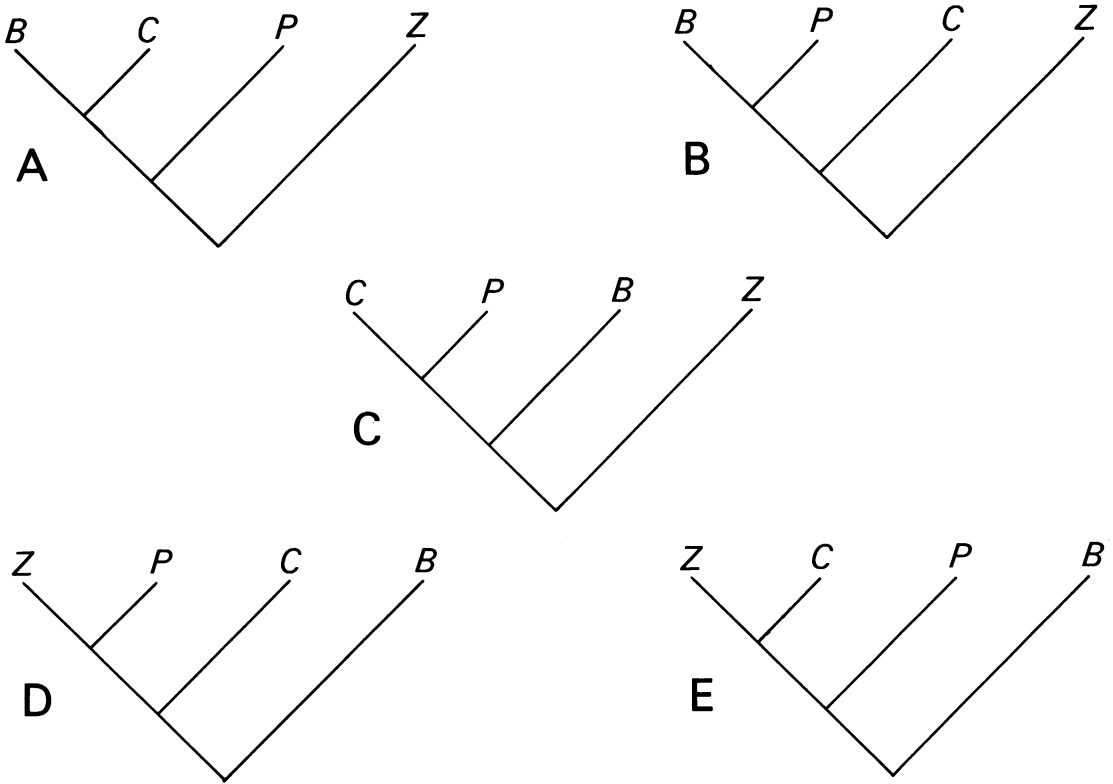


Fig. 14. Alternative hypotheses of relationships among *Bolomys lasiurus* (B), *Calomys callosus* (C), *Pseudoryzomys* (P), and *Zygodontomys* (Z). Tree A, with a length of 14 steps, is the most parsimonious cladogram supported by the data in table 3; trees B–E are each 15 steps long. Branch lengths are arbitrary and do not represent any estimated parameter of phylogeny.

confident basis for phylogenetic inference. Among these five nearly equivalent cladograms there is no informative consensus. Because the morphological evidence of relationships thus appears ambiguous in the aggregate, closer attention to individual characters is appropriate.

Among the comparisons described above, the occurrence of the gall bladder is especially interesting and merits a broader taxonomic survey. A reservoir for hepatic secretions, the gall bladder is anatomically remote from the craniodental attributes emphasized in most muroid classifications and perhaps enjoys some measure of independence from functional and developmental constraints that might cause character covariation in the head skeleton. Based on my observations, the gall bladder appears to be either unambiguously present in all conspecifics, or it is consistently and unambiguously absent. The assumed hy-

pothesis of polarity appears plausible from outgroup considerations (Vorontsov, 1979; Carleton, 1980), and *Zygodontomys* exhibits the derived state. Information about the occurrence of the gall bladder was obtained from dissections of 354 specimens representing 90 species in 47 genera and subgenera of Neotropical Sigmodontinae (table 4 and Appendix 2); all currently recognized tribes are included in this survey except the Wiedomyini.

Despite the generally unsatisfactory empirical status of Neotropical muroid classification (see Carleton and Musser, 1989: 52–55, for a critical appraisal) and the traditional taxonomic emphasis on craniodental characters, several examples of classificatory correspondence with the distribution of gall bladders are striking. (1) Fifteen genera in this survey are represented by two or more species each, but only one (*Akodon*) exhibits variation in the occurrence of the gall bladder; this

observation, together with the lack of intra-specific variation noted above, suggests that the character is conservative at lower taxonomic levels. (2) All phyllotines dissected (12 of 13 known genera are represented in this survey) possess a gall bladder, as do both scapteromyine genera examined. (3) Within the tribe Oryzomyini, members of the "oryzomyine group" (sensu Hershkovitz, 1944, 1960) lack gall bladders without exception.⁴

While such examples of congruence are encouraging, other patterns of taxonomic distribution suggest either that the gall bladder has been lost independently in several tribes or that the current tribal classification does not accurately reflect phylogenetic relationships. Since a comprehensive analysis of Neotropical muroid relationships is beyond the scope of this report, it will only be possible here to suggest which of these alternatives appears plausible in each case.

Ichthyomyini is the only Neotropical muroid tribe for which evidence of monophyly and cladistic analyses of the included species are available (Voss, 1988). Those results suggest that the ichthyomyine ancestor possessed a gall bladder and that the absence of the organ is a synapomorphy for the species of *Ichthyomys*. Despite the lack of such an explicitly phylogenetic framework to support inference in other tribes, independent loss also seems the most reasonable hypothesis to explain the absence of gall bladders in *Akodon cursor*, *Lenoxus apicalis*, and *Rhipidomys*; these taxa belong to phenetically cohesive clusters of genera that usually possess gall bladders. By contrast, *Holochilus* (listed as a member of the tribe Sigmodontini in table 4), together with *Pseudoryzomys* and *Zygodontomys* resemble members of the "oryzomyine group" (sensu Hershkovitz, 1944, 1960) in their lack of gall bladders and in other characters as well.

Hershkovitz (1960: 514–515) described the oryzomyine group as follows:

Size and form *Mus*-like to *Rattus*-like; eyes and ears normal; hind feet of the generalized scansorial-terrestrial type, or moderately specialized for running,

swimming, or climbing; three middle digits of hind foot partly, but not always conspicuously, webbed; claws short, more or less recurved, never specialized for digging; tail always more than one-half as long as head and body combined, generally thinly haired, the scales always visible; mammae eight (two pairs pectoral, two pairs inguinal). Distance between first molars always more than length of M¹; median longitudinal palatal ridge not present; bony palate produced posteriorly beyond plane of last molars; posterolateral palatal fossa present and marked by a distinct pit or reticulation of pits; parapterygoid fossa shallow, its anterior corner never undercut. Incisors ungrooved, generally opisthodont, never proodont; molars generally brachyodont, never distinctly hypsodont; crowns crested or terraced, never plane . . . ; mesoloph (id) present in all molars and fused with mesostyle (id) as a functional unit; procingulum of upper molars and postcingulum of lower molars present and usually well developed.

Although the foregoing appears to provide impressive documentation for the phenetic distinctiveness of oryzomyines, many of the listed attributes (e.g., "claws short, more or less recurved, never specialized for digging") serve to exclude just a handful of species among the known hundreds of Neotropical muroids; others are uninterpretable (e.g., "size and form *Mus*-like to *Rattus*-like"); and a few are equivocal (e.g., "three middle digits of hindfoot partly . . . webbed"). Of greater relevance, however, is the observation that all but one of these "oryzomyine" attributes are widely believed to represent primitive muroid traits (see Hershkovitz, 1962; Carleton, 1980; and Voss, 1988, for discussions of character polarities). The only character state cited above that is currently believed to be derived is the possession of a long palate (i.e., one produced behind the last molars) with prominent posterolateral pits; this putative synapomorphy, however, is also shared with some non-oryzomyine taxa including *Holochilus* (see Hershkovitz, 1955: pl. 23, 24), *Pseudoryzomys* (this report: fig. 5D), and *Zygodontomys*.

The first examples of *Zygodontomys* to be described (by Allen and Chapman, 1893; Thomas, 1894; and Allen, 1895) were originally placed in the genus *Oryzomys*, as was *Pseudoryzomys wavrini* (a junior synonym of *P. simplex*; see Voss and Myers, 1991). All of these taxa were removed from *Oryzomys* for essentially the same reason: they lack well-developed mesolophids and mesolophids. Although *Zygodontomys* and *Pseudoryzomys*

⁴ Vorontsov (1979) reported the gall bladder as present in *Oligoryzomys flavescens* and *Nectomys squamipes*, but my dissections revealed no trace of a gall bladder in either species.

TABLE 4
Distribution of the Gall Bladder Among
Neotropical Sigmodontinae
(The generic and tribal classification follows
Reig, 1984, except as noted.)

Taxon	N ^a	Gall bladder
Tribe Akodontini		
<i>Akodon (Abrothrix) longipilis</i>	2	present
<i>A. (Akodon) azarae</i>	2	present
<i>A. (A.) boliviensis</i>	2	present
<i>A. (A.) cursor</i>	10	absent
<i>A. (A.) dayi</i>	2	present
<i>A. (A.) toba</i>	2	present
<i>A. (A.) urichi</i>	5	present
<i>A. (Chroeomys) jelskii</i>	5	present
<i>Bolomys lasiurus</i>	12	present
<i>Chelemys macronyx</i>	2	present
<i>Geoxus valdivianus</i> ^b	2	present
<i>Lenoxus apicalis</i>	4	absent
<i>Microxus bogotensis</i>	12	present
<i>M. mimus</i>	10	present
<i>Oxymycterus delator</i>	5	present
<i>Podoxomys roraimae</i>	5	present
Tribe Ichthyomyini		
<i>Anotomys leander</i>	7	present
<i>Chibchanomys trichotis</i> ^c	3	present
<i>Ichthyomys hydrobates</i>	3	absent
<i>I. pittieri</i>	2	absent
<i>I. tweedii</i>	8	absent
<i>Neusticomys monticolus</i>	5	present
<i>N. venezuelae</i> ^d	4	present
<i>Rheomys mexicanus</i>	4	present
<i>R. raptor</i>	4	present
<i>R. thomasi</i>	2	present
<i>R. underwoodi</i>	4	present
Tribe Oryzomyini (Oryzomyine group) ^e		
<i>Melanomys caliginosus</i> ^f	3	absent
<i>Microrizomys altissimus</i> ^g	4	absent
<i>M. minutus</i> ^g	1	absent
<i>Neacomys tenuipes</i>	3	absent
<i>Nectomys squamipes</i>	5	absent
<i>Nesoryzomys narboroughi</i>	1	absent
<i>Oecomys bicolor</i>	1	absent
<i>O. flavicans</i>	1	absent
<i>O. speciosus</i>	1	absent
<i>O. trinitatus</i>	2	absent
<i>Oligoryzomys chacoensis</i> ^h	5	absent
<i>O. delticola</i> ^h	6	absent
<i>O. flavescens</i> ^h	1	absent
<i>O. fulvescens</i> ^h	6	absent
<i>O. microtis</i> ^h	7	absent
<i>Oryzomys (Macruroryzomys)</i> <i>hammondi</i>	1	absent
<i>O. (Oryzomys) albigularis</i>	4	absent

TABLE 4—(Continued)

Taxon	N ^a	Gall bladder
<i>O. (O.) alfaro</i>	2	absent
<i>O. (O.) capito</i>	5	absent
<i>O. (O.) macconnelli</i>	2	absent
<i>O. (O.) palustris</i>	7	absent
<i>O. (O.) ratticeps</i>	5	absent
<i>O. (O.) talamancae</i>	1	absent
<i>O. (O.) xantheolus</i>	3	absent
<i>Scolomys melanops</i>	1	absent
<i>Sigmodontomys alfari</i> (Thomasomyine group) ^f	3	absent
<i>Aepeomys lugens</i>	2	present
<i>Chilomys instans</i>	5	present
<i>Delomys dorsalis</i>	5	present
<i>Rhipidomys couesi</i>	2	absent
<i>R. fulviventer</i>	3	absent
<i>R. leucodactylus</i>	1	absent
<i>R. macconnelli</i>	10	absent
<i>R. mastacalis</i>	8	absent
<i>Thomasomys aureus</i>	5	present
<i>T. baeops</i>	6	present
<i>T. daphne</i>	2	present
<i>T. hylophilus</i>	3	present
<i>T. laniger</i>	2	present
<i>T. paramorum</i>	5	present
<i>T. rhoadsi</i>	2	present
<i>T. sylvestris</i>	3	present
Tribe Phyllotini		
<i>Andalgalomys pearsoni</i>	2	present
<i>Andinomys edax</i>	2	present
<i>Auliscomys pictus</i>	3	present
<i>Calomys callosus</i>	6	present
<i>Chinchillula sahamae</i>	2	present
<i>Eligmodontia typus</i>	2	present
<i>Euneomys petersoni</i>	1	present
<i>Graomys domorum</i>	2	present
<i>G. griseoflavus</i>	6	present
<i>Irenomys tarsalis</i>	3	present
<i>Neotomys ebriosus</i>	4	present
<i>Phyllotis amicus</i>	2	present
<i>P. andium</i>	1	present
<i>P. darwini</i>	2	present
<i>P. osilae</i>	5	present
<i>Reithrodon physodes</i>	1	present
Tribe Scapteromyini		
<i>Kunsia tomentosus</i>	3	present
<i>Scapteromys tumidus</i>	4	present
Tribe Sigmodontini		
<i>Sigmodon alstoni</i>	4	present
<i>S. hispidus</i>	5	present
<i>Holochilus brasiliensis</i>	2	absent
<i>H. magnus</i>	2	absent

TABLE 4—(Continued)

Taxon	N ^a	Gall bladder
Sigmodontinae incertae sedis		
<i>Pseudoryzomys simplex</i> ^d	1	absent
<i>Zygodontomys brevicauda</i>	22	absent

^a Number of specimens dissected in this survey.

^b *Geoxus* was resurrected from synonymy with *Notiomys* by Pearson (1984).

^c Formerly *Anotomys trichotis*, see Voss (1988).

^d *Daptomys* (including *D. venezuelae*) is regarded as a subjective synonym of *Neusticomys* following Voss (1988).

^e After Hershkovitz (1944, 1960).

^f *Melanomys*, usually ranked as a subgenus of *Oryzomys*, contains morphologically and ecologically distinctive species and merits generic status.

^g *Microrizomys*, formerly a subgenus of *Oryzomys*, was elevated to generic rank by Carleton and Musser (1989).

^h *Oligoryzomys*, formerly another subgenus of *Oryzomys*, was also elevated to generic rank by Carleton and Musser (1989) whose review of the included species is followed here.

ⁱ As characterized by Hershkovitz (1966).

^j *Pseudoryzomys* was removed from the tribe Phyllotini by Olds and Anderson (1989).

resemble oryzomyines in most of the other characteristics listed above (insofar as those attributes are interpretable or not actually misleading), Hershkovitz (1962) referred both genera to the phyllotine group, assignments that have not been supported by subsequent surveys of phyllotine penis morphology (Hooper and Musser, 1964), karyotypic variation (Pearson and Patton, 1976; Voss and Myers, 1991), and craniodental traits (Olds and Anderson, 1989).

Controversy has also surrounded the possibly close relationship of *Holochilus* to oryzomyines. From their comparisons of the glans penis among Neotropical muroids, Hooper and Musser (1964: 45) remarked that

... specimens of *Holochilus brasiliensis* are unlike examples of *Sigmodon*, the genus with which *Holochilus* has been associated ... They closely resemble oryzomyines in all respects except absolute size ... This striking and apparently fundamental resemblance of *Holochilus* and *Oryzomys* suggests that the position of *Holochilus* be reexamined with the thought in mind that it may be a well differentiated oryzomyine rather than a sigmodont.

In rejecting this hypothesis, Hershkovitz (1966) cited his revision of *Holochilus* (Hershkovitz, 1955) wherein the occurrence of "functional" mesoloph and mesolophid is emphasized (1955: 644–645) as unambiguously distinguishing sigmodonts (then understood to include *Neotomys* and *Reithrodontomys* as well as *Sigmodon* and *Holochilus*) from oryzomyines and other "primitive" New World muroids.

Hershkovitz's (1962) assignment of *Zygodontomys* and *Pseudoryzomys* to the phyllotine group and his (1966) defense of sigmodont membership for *Holochilus* were based on a theory of dental evolution and adaptive radiation that precluded any close relationships among these genera and oryzomyines. According to this interpretation (fig. 15), Neotropical muroids with complex phalli consist of two lineages, one with pentalophodont molar occlusal patterns complicated by the presence of well-developed ("functional") mesoloph and mesolophids,⁵ the other with tetralophodont molar morphologies simplified by reduction or loss of the mesoloph and mesolophid. Neotropical muroids with pentalophodont molars were regarded as primitive and generally forest-dwelling (sylvan), whereas muroids with tetralophodont molars inhabiting grasslands or other kinds of nonforest (pastoral) vegetation were interpreted as "progressive." Since Hershkovitz believed that diet, masticatory function, and life history characteristics are also involved in the complex of attributes by which pentalophodont and tetralophodont species have adapted to their respective environments, the presence or absence of the mesoloph and mesolophid served conveniently to define a fundamental evolutionary and ecological dichotomy in his view of the Neotropical muroid fauna.

⁵ "Pentalophodont" refers to the five lophs or transverse crests present on these complex teeth: anteroloph, paraloph, mesoloph, metaloph, and posteroloph in the upper dentition; anterolophid, metalophid, mesolophid, entolophid, and posterolophid in the lower dentition (names of molar occlusal structures here as elsewhere follow Reig, 1977). Well-developed or "functional" mesoloph(id)s are those that extend all the way from the median mure(id) to fuse with a small mesostyle on the labial margin of upper teeth or a mesostylid on the lingual margin of lower teeth.

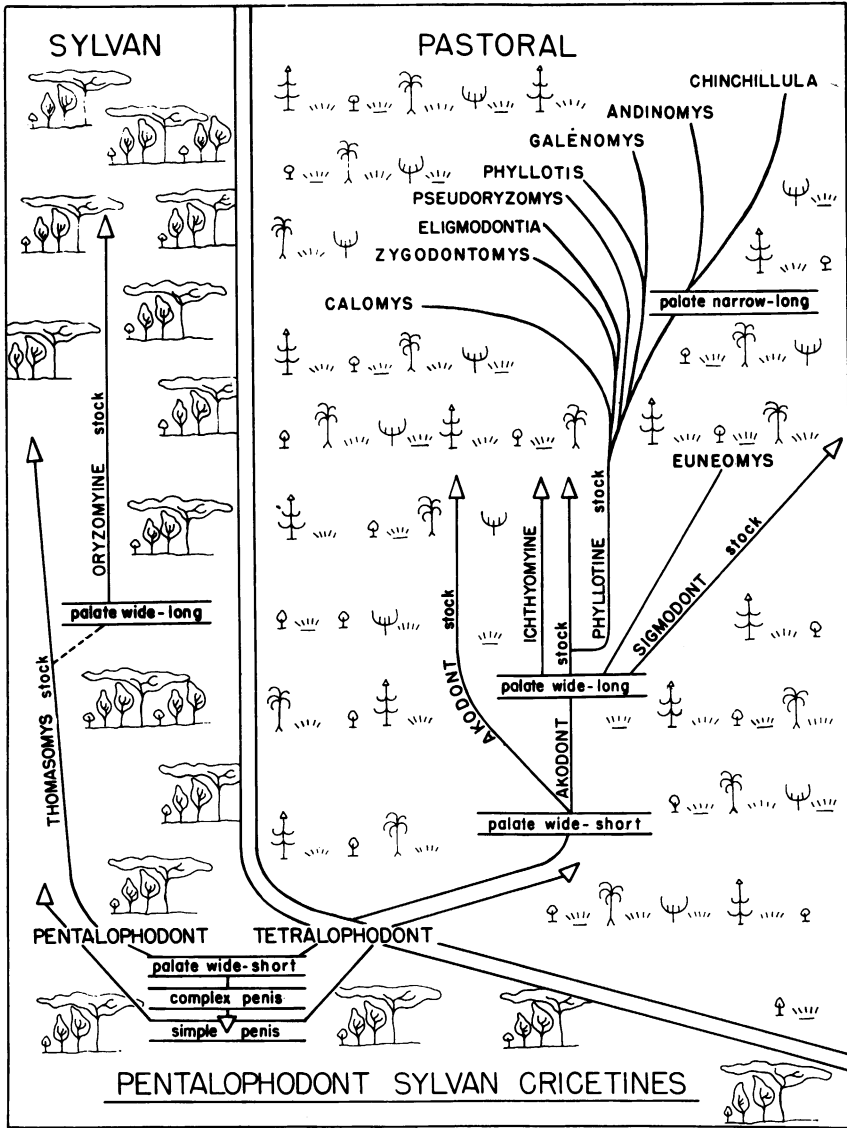


Fig. 15. A hypothesis of adaptive radiation for South American muroid rodents (reproduced from Hershkovitz, 1962: fig. 2).

Although Hershkovitz's adaptive scenario is seldom explicitly cited in the current systematic literature, mesolophs and mesolophids are, in effect, still emphasized by recent suprageneric classifications. Reig (1980), for example, attempted to consolidate the groups informally recognized by Hershkovitz into a smaller number of tribes, using names originally proposed by Vorontsov (1959). In so doing, Reig combined Hershkovitz's "thomasomyines" and "oryzomyines" into the

tribe Oryzomyini, but no discussion or analysis of character data was advanced to support this action. In fact, Reig's Oryzomyini corresponds to Hershkovitz's pentalophodont division, and the tribe is therefore united by plesiomorphic resemblance in a single character complex.

It is not the purpose of this report to propose a new suprageneric classification of Neotropical muroids, but it is appropriate to question the biological assumptions upon

which the current tribal-level taxonomy is implicitly based. Even if it were possible to establish valid ecological generalities concerning pentalophodont and tetralophodont muroids, it does not then follow that mesoloph and mesolophids could not be lost independently in convergent lineages (or that such losses are irreversible). For example, the distribution of the gall bladder (as interpreted above) invites consideration of the hypothesis that *Zygodontomys*, *Pseudoryzomys*, and *Holochilus* belong to a clade that includes Hershkovitz's oryzomyine group but not tho-

masomyines or members of other Neotropical muroid tribes. If such a clade were primitively pentalophodont, and if *Zygodontomys*, *Pseudoryzomys*, and *Holochilus* are not each other's closest relatives, this would imply several independent reductions or losses of the mesoloph and mesolophid. Future cladistic analyses incorporating broader taxonomic surveys of other morphological characters, karyotypes,⁶ and molecular data may lend credence to these conjectures or compel acceptance of better corroborated alternatives.

VARIATION WITHIN AND AMONG POPULATIONS

The discrimination of closely related species requires that normal patterns of variation within populations be distinguished from patterns of interpopulation variation that may reflect the genetic divergence of reproductively isolated lineages. It is, of course, seldom possible to prove the genetic basis of differences observed among population samples, but to the extent that other factors can be taken into account, systematic inference is strengthened. Information is provided below concerning variation within and among populations for pelage color and craniodental measurements, characters that have often been used in the past to diagnose species and subspecies of *Zygodontomys*.

PELAGE

Very young *Zygodontomys* (usually with unerupted or unworn third molars) exhibit a juvenile pelage that is dull, softer, and darker than the mature coat. Hair replacement begins laterally and progresses dorsally; the newly molted areas join in the middle of the back and then spread caudally and rostrally. Therefore, some young specimens are covered by a bright, new, mature coat on the back and sides but retain the dull, darker juvenile pelage over the rump, shoulders, and head. Very old specimens often have white hairs or irregular whitish spots scattered throughout the pelage.

Apart from these ontogenetic changes, most pelage color variation in large population samples appears uncorrelated with any tan-

gible cause (e.g., sex, evidence of disease, etc.). Within otherwise homogeneous series, individuals vary according to the amount (saturation) of yellow or reddish hues in the fur; for example, from deep olive-yellow to pale grayish. Occasional specimens in predominantly grayish series may have distinctly reddish fur, and vice versa. Usually, specimens that are yellower or redder than average dorsally are also washed ventrally with similar tints.

In most samples there is also individual variation in the coarseness of grizzling and in the overall darkness of the fur. Both effects appear to be independent of variation in red and yellow pigments and may reflect the thickness or density of dark guard hairs or the length of dark tips on buff-banded awn hairs.

There are obvious differences among populations in pelage color. For example, the forest-dwelling populations of Isla San Miguel

⁶ Reig et al. (1990) recently concluded that "... karyological data strongly support the hypothesis that *Zygodontomys* is closely linked to the early radiation of the oryzomyini, and is better classified within that tribe as originally held by Tate." Unfortunately, the cited chromosomal data are phylogenetically ambiguous since high diploid numbers (such as those of *Zygodontomys* and some oryzomyines) may be primitive for Neotropical muroids (Gardner and Patton, 1976; Reig et al., 1990; but see Baker et al., 1983). Meaningful systematic interpretations of karyological comparisons must await more sophisticated analyses that convincingly establish chromosome-arm homologies among the taxa of interest and relevant outgroups.

(Panama), Trinidad, and Tobago are more richly pigmented (in deep yellowish or reddish tones) than are savanna-dwelling populations from adjacent mainland localities. Specimens from arid continental landscapes are usually paler than specimens collected in regions of higher rainfall, and other ecogeographic regularities could perhaps be demonstrated with careful colorimetric studies.

The classic descriptions of geographic variation in North American mammals (e.g., by Dice and Blossom, 1937; Hooper, 1941; and Blair, 1947) in conjunction with experimental research using captive breeding stocks of *Peromyscus* (summarized by Sumner, 1932, and reanalyzed by Wright, 1978; see also Hayne, 1950) documented the Mendelian basis for population differences in pelage pigments, the probable origin of such differences by predation-mediated natural selection (see especially Dice, 1945, 1947), and the local dilution of the effects of selection by gene flow. Although detailed investigations along these lines have seldom been repeated, it is reasonable to assume that similar factors may be causally responsible for pelage color variation among most populations of small mammals, including *Zygodontomys*. Even with these biological insights, however, the taxonomic utility of integumental pigments is still largely dictated by the pragmatic issue of effective discrimination.

Pelage-color comparisons were extensively employed in the early taxonomic literature, frequently on the basis of just one or a few skins from local populations. Allen (1913), for example, mentioned only size and pelage color to distinguish *Zygodontomys griseus* from *Z. fraterculus* (as represented by one and two specimens, respectively), but the cited color (and size) differences fall well within the normal range of variation exhibited by most large population samples. Even when pelage-color differences between adequate samples are pronounced, however, they seldom provide a sufficient basis for unambiguous diagnosis because of overlapping variation. Since color is, additionally, laborious to quantify, and because populations that differ in color are often not phenotypically distinguishable in other characters, pelage comparisons are not emphasized in the following species accounts.

CRANIAL AND DENTAL MEASUREMENTS

Quantitative comparisons of skulls and teeth have traditionally been emphasized in muroid systematics and craniodental measurements provide important evidence of evolved differences among populations of *Zygodontomys*. Univariate descriptive statistics for a large sample from El Dividive, Venezuela (table 5) represent typical patterns of variation within populations. The observed range in cranial length (CIL) is usually about 6 or 7 mm among adults (TWC 2–4) of both sexes; in absolute terms, within-sample variation is substantially less for other cranial dimensions, but indices of relative variability are more biologically informative. Coefficients of variation (sample standard deviations expressed as percentages of sample means) are large for most measurements of the facial skull (LD, BR, BPB, BZP) and of the incisors (DI). By contrast, molar dimensions (LM, BM1) and measurements of the neurocranium (LIB, BB) are relatively much less variable. Overall cranial length (CIL) and dimensions of the incisive foramina (LIF) and of the orbits (LOF) usually exhibit intermediate coefficients of variation.

Pairwise correlations (table 6) reveal similar contrasts among craniodental dimensions. Correlations among measurements of the facial skull and incisors are always large and positive, while correlations involving measurements of the molar dentition are substantially smaller; neurocranial correlations are of intermediate magnitude.

Analyses of variance based on toothwear class and sex (table 7) suggest that observed differences among craniometric characters in relative variability and correlation have an ontogenetic basis. For population samples with sufficiently balanced representation by specimens among toothwear and sex classes to permit reasonable estimation of variance components (as recommended by Leamy, 1983), sex usually contributes less than 10 percent to the total variance in any character. Age (as indexed by toothwear), however, consistently accounts for a substantial fraction of the total variance in all but four craniodental dimensions (LM, BM1, LIB, BB). Sex

TABLE 5
Descriptive Statistics for Craniodental Measurements (in millimeters) of 68 Adult Specimens of *Zygodontomys brevicauda* from El Dividive (Venezuelan locality 72)

	Mean	Observed range	Standard deviation	Coef- ficient of variation
CIL	27.4	23.0–30.7	1.64	6.0
LD	7.8	6.2–8.9	0.61	7.8
LM	4.2	3.9–4.6	0.17	4.0
BM1	1.3	1.2–1.4	0.05	3.8
LIF	6.1	5.0–7.2	0.45	7.4
BR	4.9	3.9–5.8	0.42	8.6
BPB	2.9	2.2–3.6	0.28	9.7
BZP	3.0	2.4–3.7	0.29	9.7
LIB	4.7	4.2–5.4	0.26	5.5
BB	12.2	11.2–12.8	0.39	3.2
DI	1.6	1.2–1.8	0.15	9.4
LOF	10.2	8.5–11.4	0.61	6.0

× age interaction terms are negligible in most analyses.

Laboratory breeding studies with *Zygodontomys* (Voss et al., 1990) provided unambiguous experimental evidence that age-correlated growth causes substantial increases in many cranial dimensions long after the molar dentition has erupted. Growth of the facial skeleton and the incisors is indeterminate and continues throughout adulthood. The neurocranium, however, completes growth earlier in postnatal life; measure-

TABLE 7
Percentage of Total Variance (calculated from variance components) Partitioned Among Sex, “Age” (= toothwear class) and Interaction for Craniodental Measurements of 68 Adult *Zygodontomys brevicauda* from El Dividive (Venezuelan locality 72)

	Sex	“Age”	Sex × “Age”	Error
CIL	8.8	44.5	0.0	46.7
LD	8.8	42.5	0.0	48.7
LM	0.0	9.8	0.1	90.1
BM1	1.5	0.0	0.0	98.5
LIF	0.4	28.3	4.1	67.1
BR	0.0	32.9	8.9	58.2
BPB	0.0	54.8	1.2	44.0
BZP	0.0	48.6	7.0	44.3
LIB	5.0	11.7	9.1	74.2
BB	0.0	14.1	0.0	85.9
DI	6.0	47.8	0.0	46.2
LOF	7.0	31.1	0.0	62.0

ments of the braincase and interorbit therefore increase only slightly after molar eruption is completed. Since erupted molars do not grow, the skulls of young adults are characterized by precociously large neurocrania and molar rows but immature, diminutive rostra and feeble zygomatic arches. By contrast, the neurocranium and molars of older animals are proportionately smaller as a consequence of prolonged (positive allometric) growth in the facial skeleton (fig. 16).

Populations of *Zygodontomys* do not ex-

TABLE 6
Matrix of Pairwise Correlations Among Craniodental Measurements of 68 Adult Specimens of *Zygodontomys brevicauda* from El Dividive (Venezuelan locality 72)

LD	0.96*										
LM	0.23	0.09									
BM1	0.09	0.06	0.50*								
LIF	0.80*	0.83*	0.05	0.06							
BR	0.79*	0.76*	0.27*	0.62*							
BPB	0.82*	0.82*	0.10	0.06	0.68*	0.78*					
BZP	0.77*	0.74*	0.25*	0.10	0.66*	0.67*	0.73*				
LIB	0.66*	0.63*	0.36*	0.20	0.53*	0.69*	0.60*	0.51*			
BB	0.60*	0.61*	−0.04	−0.02	0.60*	0.48*	0.58*	0.40*	0.44*		
DI	0.84*	0.76*	0.28*	0.15	0.63*	0.74*	0.77*	0.66*	0.53*	0.51*	
LOF	0.93*	0.89*	0.18	0.06	0.76*	0.75*	0.74*	0.71*	0.57*	0.62*	0.80*
CIL	LD	LM	BM1	LIF	BR	BPB	BZP	LIB	BB	DI	

* $p \leq 0.05$.

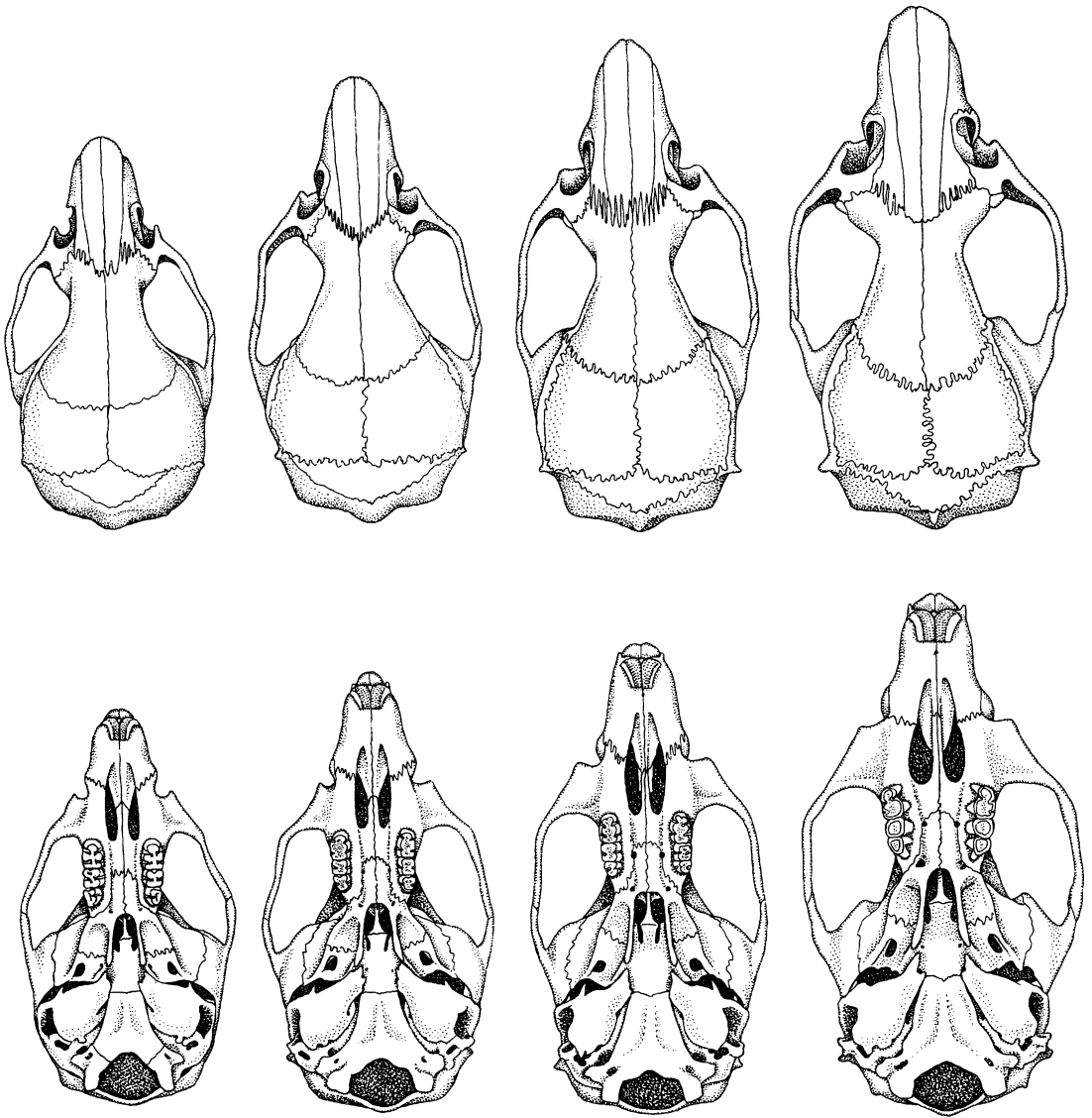


Fig. 16. Allometric cranial growth of *Zygodontomys brevicauda* from Finca Vuelta Larga (Venezuelan locality 69). From left, toothwear class (TWC) 1 (AMNH 257333), TWC 2 (AMNH 257330), TWC 3 (AMNH 257331), TWC 4 (AMNH 257323).

hibit conspicuous reproductive seasonality (see Natural History, below) and most large samples therefore contain juveniles, old adults, and specimens in each of the three adult toothwear classes. Samples of 20 or more adults are usually comparable to the extent that TWC 2, 3, and 4 each contain several specimens and TWC 3 is the modal or median class. Univariate measures of central tendency and dispersion provide a heu-

ristic basis for judging resemblances among such samples, but assumptions required by most univariate inferential statistics (e.g., of independent, normally distributed observations) are unlikely to be satisfied except in tests for differences in molar and neurocranial dimensions unaffected by age-correlated growth. Multivariate sample comparisons involve other assumptions, some of which are discussed in Materials and Methods.

SPECIES ACCOUNTS

ZYGODONTOMYS BRUNNEUS
THOMAS

Zygodontomys brunneus Thomas, 1898: 269.

Zygodontomys brevicauda brunneus Gyldenstolpe, 1932: 112.

Oryzomys (Micronectomys) borrori Hernandez-Camacho, 1957: 223.

TYPE MATERIAL: The holotype (BMNH 98.7.3.4) consists of the overstuffed skin of an adult female unaccompanied by any skeletal elements; small patches of fur are missing from the dorsum and venter, but the integument is otherwise intact. Another specimen (BMNH 98.7.3.5), consisting of a skull with mandibles and identified by Thomas's handwritten label as the paratype, is that whose measurements accompany those of the type skin in the published description. The label attached to the holotype gives the collection locality and date as "El Saibal, W. Cundinamarca, 22 Dec. 1895," but the label attached to the paratype is undated and only provides "W. Cundinamarca" as the collection locality; both specimens were collected by G. D. Child. I have not been able to locate "El Saibal" in any Colombian gazetteer or on any map of Departamento Cundinamarca. Western Cundinamarca consists chiefly of lowlands in the valley of the upper Río Magdalena, but since other Child specimens labeled "W. Cundinamarca" belong to species known elsewhere only from montane habitats (e.g., *Chibchanomys trichotis*, see Voss, 1988: 321–322), there is some reason to doubt the geographical accuracy of this collector's data.

Thomas (1898) reported the length of the "wet" hindfoot of BMNH 98.7.3.4 as 25 mm, but even allowing for the British practice of measuring hindfeet *sin unguis* (without claws), this value must be erroneous. My measurement of the dry hindfoot *con unguis* is 30 mm, but the true length of the fresh, flexible foot could have been slightly greater.

It is possible that BMNH 98.7.3.4 and 98.7.3.5 are parts of the same individual, but Thomas (1898) did not explicitly state that inference. The label attached to the skull notes "Tied to wrong skin," suggesting that Thomas had identified a mismatch, perhaps orig-

inally created in the field by Child. Unless Thomas believed that the skin and skull actually belonged to the same individual, it is hard to see why he would have associated them with apparent confidence. Fortunately, numerous complete preparations in other museums are available to confirm that BMNH 98.7.3.4 and 98.7.3.5 are correctly associated as belonging to the same biological species.

DISTRIBUTION AND SYMPATRY: Known only from the intermontane valleys of Colombia including those of the upper Río Magdalena (south of about 7°N), the upper Río Cauca, the upper Río Patía, and the upper Río Dagua. Elevations of collection localities recorded on specimen labels, in field notes, or in the published literature range from 350 to 1300 m above sea level.

Zygodontomys brunneus occurs sympatrically with *Z. brevicauda* in the upper Magdalena valley; localities where both species have been collected together are Caparrapí (Colombian locality 18) in Departamento Cundinamarca and the Valle de Suaza (locality 21) in Departamento Huila (see fig. 2). Elsewhere, in the valleys of the Río Cauca, the Río Patía, and the Río Dagua, *Z. brunneus* apparently occurs without any sympatric congeners.

MORPHOLOGICAL CHARACTERS: A species of *Zygodontomys* distinguished from sympatric populations of *Z. brevicauda* by its much larger size; additionally, *brunneus* is distinguished by its more hypsodont molars with oblique mures and murids, less opisthodont upper incisors, shallower zygomatic notches, less inflated nasolacrimal capsules, small but (usually) persistent sphenopalatine vacuities, and complete stapedial circulation (pattern 1 of Voss, 1988).

KARYOTYPES: Unknown.

COMPARISONS: The existence of two biological species of *Zygodontomys* in the valley of the upper Río Magdalena is indicated by the bimodal distribution of measurements of specimens collected from the same or adjacent localities and by the correlated variation of qualitative osteological and pelage characters. Specimens from the upper Magdalena valley are easily sorted by these criteria into

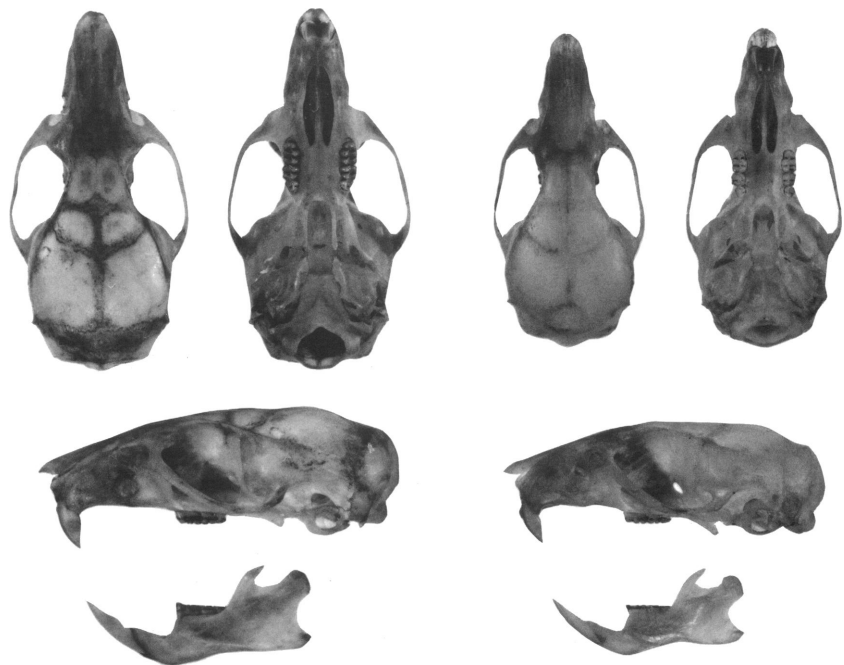


Fig. 17. Sympatric species of *Zygodontomys* from the upper Río Magdalena valley. Left, *Z. brunneus* (USNM 541909); right, *Z. brevicauda* (MVZ 113379).

TABLE 8
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brunneus* and *Z. brevicauda* from the Upper Magdalena Valley of Colombia

	<i>Z. brunneus</i>		<i>Z. brevicauda</i> ^d
	Paratype ^b	Other specimens ^c	
CIL	32.3	29.0 ± 1.91 (26.0–33.0)	25.6 ± 1.54 (22.8–28.6)
LD	9.4	8.5 ± 0.81 (7.2–10.5)	7.4 ± 0.62 (6.3–8.7)
LM	4.9	4.8 ± 0.16 (4.6–5.2)	4.2 ± 0.16 (3.8–4.4)
BM1	1.4	1.5 ± 0.07 (1.4–1.8)	1.3 ± 0.05 (1.2–1.4)
LIF	7.2	6.8 ± 0.58 (5.9–8.6)	6.0 ± 0.48 (5.0–6.8)
BR	5.8	5.1 ± 0.41 (4.4–6.0)	4.7 ± 0.28 (4.2–5.0)
BPB	3.4	3.1 ± 0.35 (2.5–3.9)	2.8 ± 0.21 (2.4–3.1)
BZP	3.6	3.1 ± 0.30 (2.5–3.6)	2.8 ± 0.28 (2.4–3.5)
LIB	5.1	5.0 ± 0.21 (4.6–5.6)	4.6 ± 0.18 (4.3–4.9)
BB	13.2	12.9 ± 0.38 (12.2–13.8)	11.4 ± 0.32 (10.8–12.0)
DI	1.8	1.6 ± 0.14 (1.2–1.8)	1.4 ± 0.10 (1.3–1.6)
LOF	10.8	10.2 ± 0.61 (9.2–11.4)	9.6 ± 0.56 (8.8–10.7)

^a The mean plus or minus one standard deviation and the observed range (in parentheses).
^b BMNH 98.7.3.5.
^c Specimens with complete measurement data from Colombian localities 18, 19, 21, and 35; 16 males, 14 females, and 10 of unknown sex. This sample includes the holotype of *Oryzomys borreroi*.
^d Specimens with complete measurement data from Colombian localities 18, 21, 22, 37, and 38; 11 males, 9 females. This sample includes the holotypes of *Z. fraterculus* and *Z. griseus*.

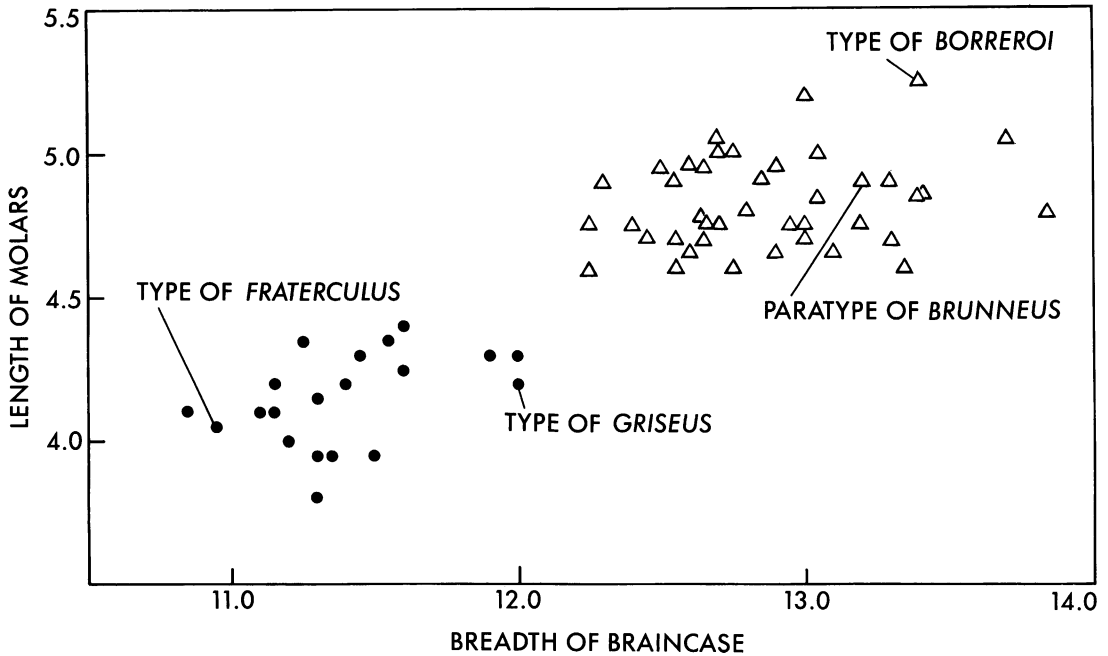


Fig. 18. Scatterplot of two craniodental measurements (mm) illustrating the morphometric discrimination of *Zygodontomys brevicauda* (●; *fraterculus* and *griseus* are included as synonyms) and *Z. brunneus* (△; including *borreroi*) based on specimens from the upper Río Magdalena valley.

two discrete clusters: one contains the type material of *Zygodontomys brunneus* and *Oryzomys borreroi*; the second includes the holotypes of *Z. fraterculus* and *Z. griseus*, both junior synonyms of *Z. brevicauda*.

Sympatric populations of *Zygodontomys brunneus* and *Z. brevicauda* can be unambiguously distinguished by craniodental measurements alone (table 8). In addition to a clear distinction in length of the upper molar series (LM), the two species do not overlap in braincase breadth (BB), and the joint distribution of these two variates (fig. 18) provides compelling evidence for discrimination.

In qualitative osteological comparisons, *Zygodontomys brunneus* is most readily distinguished from *Z. brevicauda* by molar morphology. The molars of *Z. brevicauda* are low-crowned and, in lingual view (fig. 19, top), the wide reentrant folds usually extend for only about half the depth of the unworn crown. In *Z. brunneus* (fig. 19, bottom), the molars are conspicuously more hypsodont and the reentrant folds (narrower than those of *Z. brevicauda*) usually extend from two-

thirds to three-fourths the depth of the unworn crown. The two species also differ subtly in occlusal architecture. The anterior and median mures of M1 are colinear down the central axis of the tooth in *Z. brevicauda* (fig. 20B), and the principal cusps are symmetrically disposed in opposite labial-lingual pairs to produce an overall impression of striking

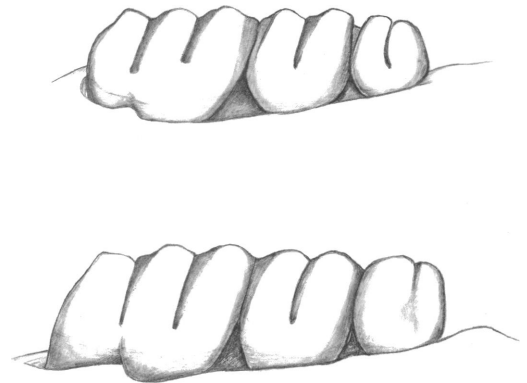


Fig. 19. Lingual view of upper molars. Top, *Zygodontomys brevicauda* (MHNLS 8233); bottom, *Z. brunneus* (AMNH 33773).

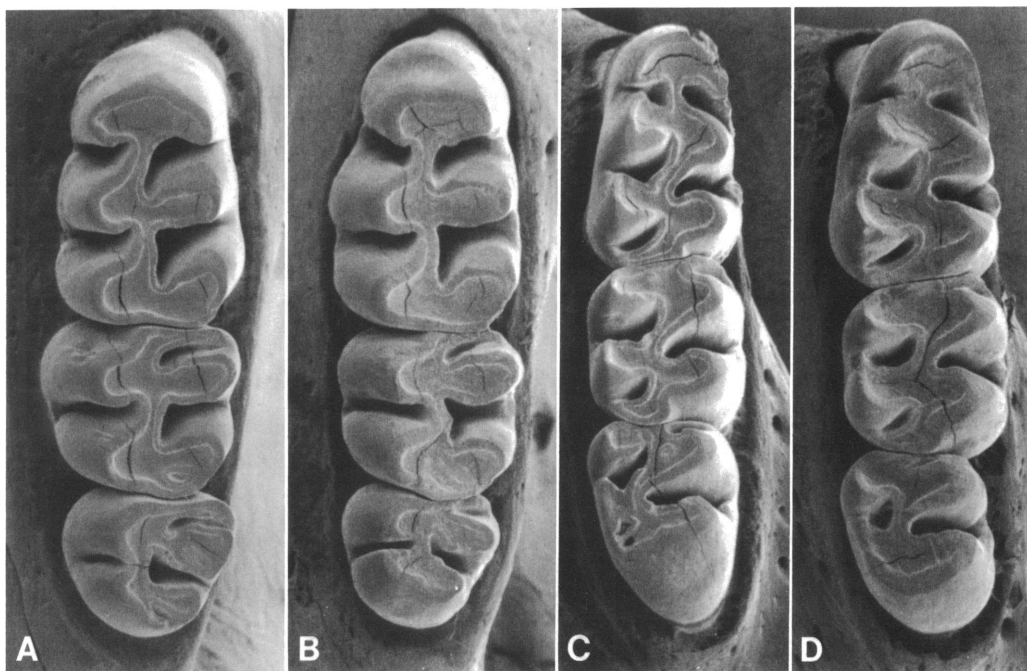


Fig. 20. Left maxillary (A, B) and right mandibular (C, D) molars of *Zygodontomys* species. A, C, *Z. brunneus* (FMNH 71258); B, D, *Z. brevicauda* (AMNH 173971).

orthogonality and simplicity. The labial reentrant folds (paraflexus and metaflexus) bend abruptly around the anteromedial aspects of the paracone and metacone, but the protoflexus and hypoflexus each run straight from the lingual margin to the midline of the tooth. By contrast, the anterior and median mures of M1 in *Z. brunneus* (fig. 20A) are not colinear down the middle of the tooth; instead, these crests are rendered oblique by small anterior deflections of the lingual reentrant folds and corresponding medial deflections of the interior parts of the labial folds. The lower molars of *Z. brevicauda* (fig. 20D) had *Z. brunneus* (fig. 20C) reveal a similar contrast, between a nearly orthogonal disposition of folds and crests in the former species and a more oblique arrangement in the latter.

Other qualitative craniodental characters contribute to species identification. The zygomatic notch is usually shallower and the nasolacrimal capsules are less inflated in *Z. brunneus* than in *Z. brevicauda*; since these structures are juxtaposed in dorsal view, the morphology of the rostrum appears conspicuously different when typical examples are

compared from this perspective (fig. 21, left). These are average differences, however, and some specimens are not unambiguously assignable to species on either character alone.

In lateral view (fig. 21, right) *Z. brunneus* and *Z. brevicauda* may be further distinguished by the more opisthodont incisors of the latter; while not actually orthodont, the exposed upper incisors of *Z. brunneus* are visibly less strongly recurved. This is another contrast that is easily illustrated with typical examples and confirmed by examination of numbers of specimens; it is best employed for identification in conjunction with other attributes, however, due to the subtlety of the difference when occasional variants of the two species are compared.

Size of the hindfoot (fig. 22) and pelage color serve as external characters by which specimens from sympatric populations of *Z. brunneus* and *Z. brevicauda* can be distinguished in the field. In the upper Magdalena valley, skins of *Z. brevicauda* are grayish; specimens from the vicinity of Villavieja (Colombian locality 23) are pale, but others (e.g., USNM 282113 from Caparrapí, Co-

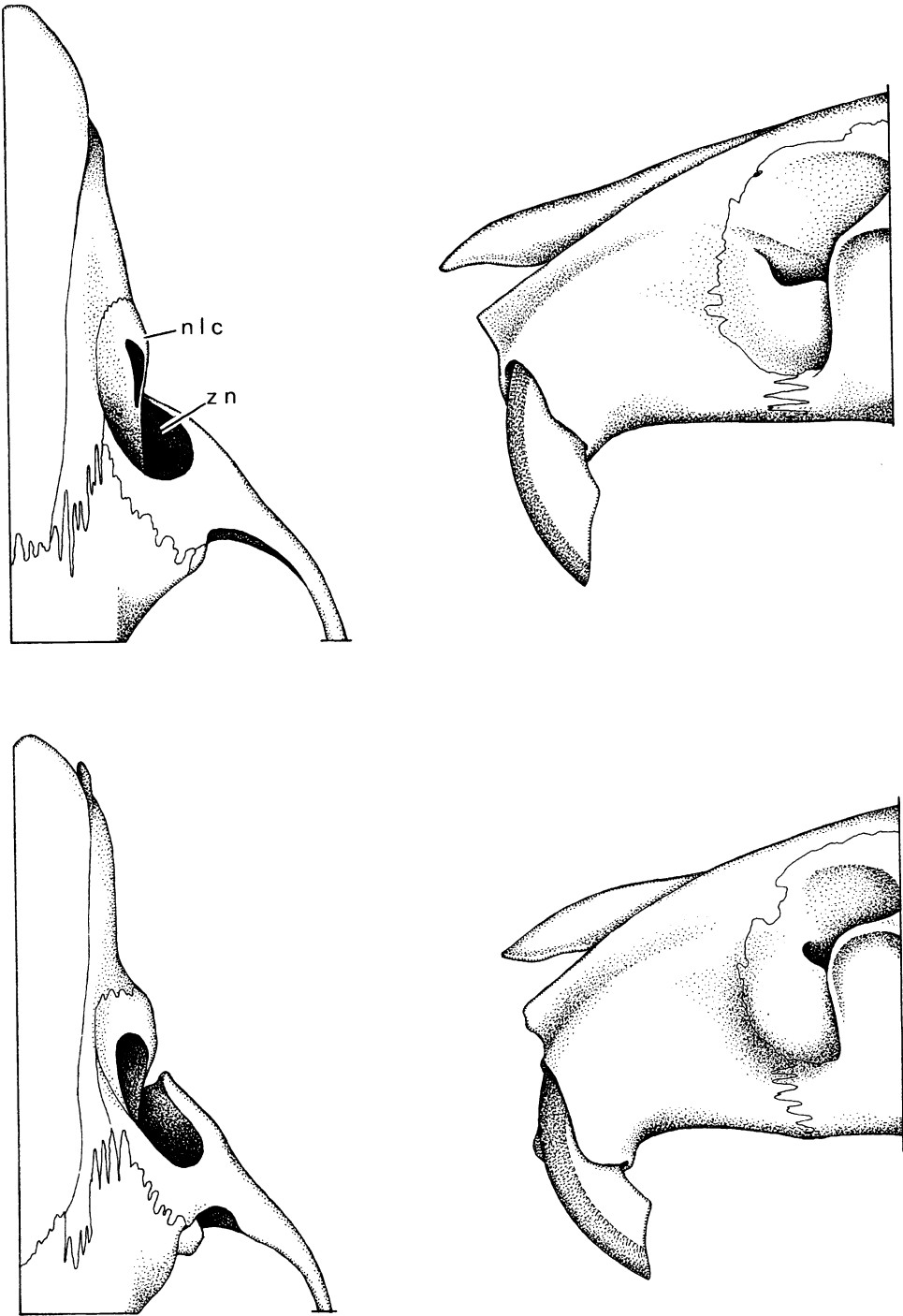


Fig. 21. Dorsal (left) and lateral (right) views of rostra. Top, *Zygodontomys brunneus* (USNM 541909); bottom, *Z. brevicauda* (MVZ 113957). nlc, nasolacrimar capsule; zn, zygomatic notch.

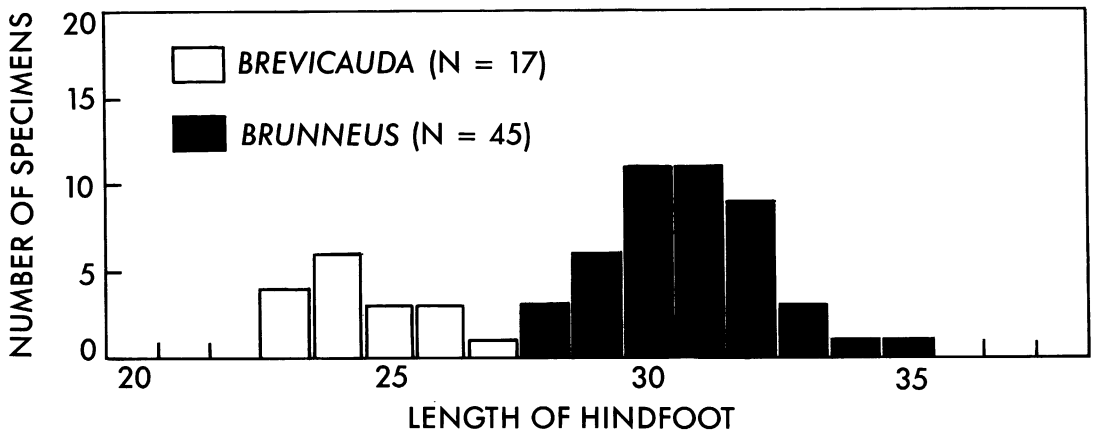


Fig. 22. Histogram of adult hindfoot measurements (in millimeters) illustrating nonoverlapping dimensions of *Zygodontomys brevicauda* and *Z. brunneus* from the upper Río Magdalena valley.

lombian locality 18) are darker; the range of dorsal hues approximates that between Smithe's (1975–1981) Drab-Gray (Color 119D) to Dark Drab (Color 199B). Ventrally, *Z. brevicauda* specimens from the upper Magdalena valley are silvery, dirty whitish, or pale buff; the ventral hairs are grayish basally but the lighter, distal colors predominate on the unruffled pelage surface. By contrast, specimens of *Z. brunneus* from the upper Magdalena valley are more richly pigmented and generally darker rats. The dorsal pelage is tawny or rufous, a range of yellow-to-reddish tones approximated by Smithe's Cinnamon (Color 123A) to Antique Brown (Color 37). Ventrally, *Z. brunneus* is conspicuously darker than sympatric *Z. brevicauda*; the dominant ventral color is gray (near Smithe's Medium Neutral Gray, Color 83), a dull plumbeous hue only superficially washed with paler, yellowish tints.

GEOGRAPHIC VARIATION: Specimens from the upper Río Magdalena valley are a morphologically homogeneous lot despite the five degrees of latitude over which they were collected. Population samples from the valleys of the Río Cauca, the Río Patía, and the Río Dagua, however, average smaller in most craniodental dimensions (table 9). Specimens from these allopatric populations are referred to *Z. brunneus* chiefly on the basis of qualitative characters, those of molar hypsodonty, occlusal morphology, and incisor curvature providing the clearest evidence of affinity. Additionally, molar dimensions (especially

LM) and braincase breadth (BB) are substantially greater in upper Cauca valley samples than in specimens of *Z. brevicauda* from the Colombian Caribbean lowlands (e.g., from Villanueva, Colombia locality 20; table 20). In the sample from Finca Arizona (table 9, last column), however, the braincase is narrow. Chromosomal and biochemical data should be collected to test the hypothesis that these allopatric western populations are conspecific with *Z. brunneus* from the upper Río Magdalena valley.

REMARKS: The type of *Oryzomys borroeroi* (ICN 418) consists of the skin and skull of an adult (TWC 4) female. Gardner and Patton (1976) first suggested that *O. borroeroi* is referable to *Zygodontomys*, and my examination of the holotype in Bogotá confirms their judgment. The specimen is large, an observation consistent with its advanced stage of toothwear, but differs in no qualitative respect from other examples of *Z. brunneus*. The type locality (Hacienda Montebello, Colombian locality 35) is the northernmost site from which *Z. brunneus* is known, however, and more material from this area could significantly contribute to knowledge of geographic variation of *Zygodontomys* in the upper Magdalena valley.

SPECIMENS EXAMINED: Colombia—Antioquia, San Jerónimo (FMNH 17); Boyacá, Muzo (FMNH 15); Cauca, Patía (ICN 1), Río Guachicón (FMNH 3); Cundinamarca, "Bogotá" (BMNH 1), Caparrapí (ICN 5, USNM 1), "El Guamito near Bogotá"

TABLE 9

Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brunneus* from the Valleys of the Río Cauca and the Río Patía, Colombia

	Río Cauca		Río Patía
	San Jerónimo ^b (8 ♂, 4 ♀)	Hacienda Formosa ^c (4 ♂, 4 ♀)	Finca Arizona ^d (13 ♂, 3 ♀)
CIL	27.0 ± 1.40 (24.8–29.0)	27.6 (25.6–29.9)	25.9 ± 1.52 (22.9–28.8)
LD	7.9 ± 0.58 (7.0–8.6)	8.1 (7.3–9.0)	7.4 ± 0.58 (6.2–8.4)
LM	4.5 ± 0.12 (4.4–4.8)	4.6 (4.5–4.8)	4.5 ± 0.17 (4.2–4.8)
BM1	1.5 ± 0.05 (1.4–1.5)	1.5 (1.5–1.6)	1.5 ± 0.07 (1.4–1.6)
LIF	6.6 ± 0.31 (6.2–7.0)	6.6 (5.8–7.2)	6.3 ± 0.32 (5.7–6.8)
BR	4.7 ± 0.30 (4.0–5.0)	4.8 (4.6–5.2)	4.5 ± 0.32 (3.9–5.1)
BPB	2.8 ± 0.41 (2.3–3.7)	3.0 (2.7–3.4)	2.7 ± 0.22 (2.4–3.1)
BZP	2.9 ± 0.28 (2.5–3.4)	3.1 (2.8–3.5)	2.9 ± 0.22 (2.6–3.3)
LIB	4.8 ± 0.24 (4.4–5.2)	4.8 (4.6–5.0)	4.6 ± 0.16 (4.4–5.1)
BB	12.6 ± 0.30 (12.1–13.1)	12.7 (12.4–13.2)	11.9 ± 0.21 (11.5–12.3)
DI	1.5 ± 0.13 (1.3–1.7)	1.6 (1.4–1.7)	1.5 ± 0.09 (1.4–1.6)
LOF	9.8 ± 0.58 (8.8–10.6)	9.9 (9.2–10.6)	9.5 ± 0.49 (8.6–10.5)

^a The mean plus or minus one standard deviation (for samples of ten or more specimens), and the observed range (in parentheses).

^b Colombian locality 3.

^c Colombian locality 41.

^d Colombian locality 33.

(BMNH 1), “El Saibal” (BMNH 1, the holotype of *brunneus*), Paime (AMNH 9, BMNH 1, USNM 4), “W. Cundinamarca” (BMNH 1, the paratype of *brunneus*); Huila, Andalucía (AMNH 1), Valle de Suaza (UVM 5, USNM 32); Nariño, Finca Arizona (UVB 19); Santander, Hacienda Montebello (ICN 1, the type of *borreroi*); Valle de Cauca, Atuncela (UVM 1), Cali (MNHN 4), Hacienda Formosa (UVB 8), Loboguerrero (UVB 1). Total, 132.

ZYGODONTOMYS BREVICAUDA

(J. A. Allen and Chapman)

Oryzomys breviceuda Allen and Chapman, 1893: 215. (Other synonyms are listed in the subspecies accounts.)

TYPE MATERIAL: The holotype consists of the separately cataloged skin (AMNH 5981) and skull with mandibles (AMNH 4708) of an adult (TWC 4) male collected by Frank M. Chapman on 12 April 1893 at “Princes-town” (= Princes Town), Trinidad. The left zygomatic arch is broken and both upper third molars are missing, but the specimen is otherwise intact.

DISTRIBUTION: As for the genus, but ex-

cluding the valleys of the upper Río Cauca, the Río Patía, and the Río Dagua in Colombia where *Zygodontomys brunneus* appears to be the only species present.

MORPHOLOGICAL CHARACTERS AND COMPARISONS: Conspicuously smaller than *Zygodontomys brunneus* where the two species are sympatric in the upper Magdalena valley of Colombia; allopatric populations of *Z. breviceuda*, however, especially those on islands, may approach or equal *Z. brunneus* in craniodental and external dimensions. In qualitative cranial characters, *Z. breviceuda* is distinguished by the distinctive occlusal morphology of its brachydont molars, more opisthodont incisors, deeper zygomatic notches, and more inflated nasolacrimal capsules as described in the preceding account for *Z. brunneus*.

KARYOTYPES: See under subspecies accounts.

GEOGRAPHIC VARIATION: Frequencies of qualitative cranial traits related to the stapedial arterial circulation and to the fenestration of the mesopterygoid fossa vary geographically among populations of *Zygodontomys breviceuda*.

The pattern of carotid supply believed

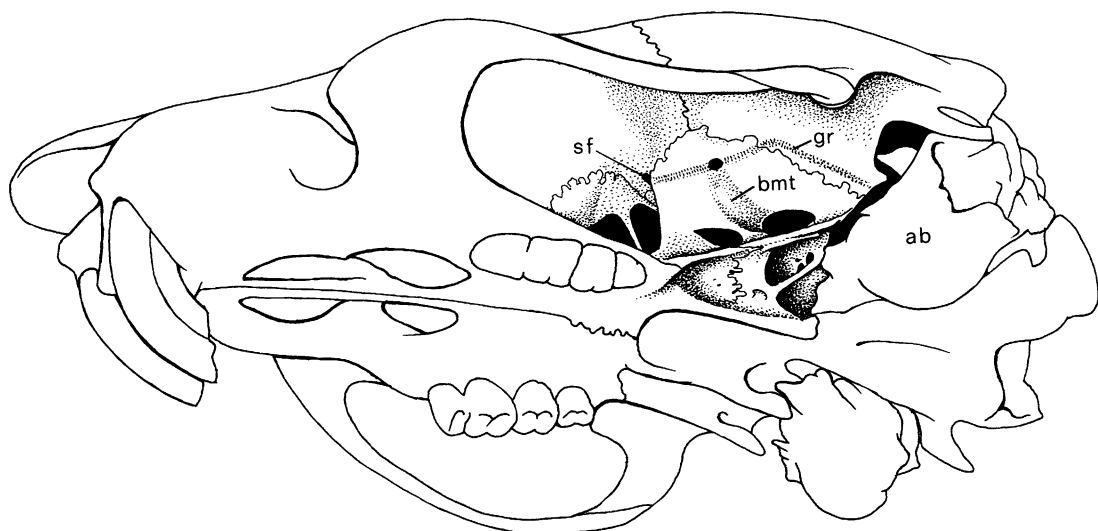


Fig. 23. Ventrolateral view of skull illustrating the osteological traces of a complete stapedial circulation (USNM 448669, *Zygodontomys brevicauda cherriei*). **ab**, auditory bulla; **bmt**, buccinator-masticatory trough; **gr**, internal groove of supraorbital stapedial ramus; **sf**, sphenofrontal foramen.

primitive for muroids (Bugge, 1970; Carleton, 1980) includes what may be termed a complete stapedial circulation. In this morphology (corresponding to pattern 1 of Voss, 1988), a large stapedial artery departs from the internal carotid and enters the middle ear through the stapedial foramen, a conspicuous perforation in the petrotympanic fissure on the posteromedial surface of the auditory bulla. Passing through the stapes, the artery exits the middle ear and enters the braincase through a cleft in the roof of the bullar capsule. The vessel passes rostrally inside the braincase to a point just above the anterior margin of the bulla where it divides into supraorbital and infraorbital branches. The supraorbital branch, whose presence characterizes this complete stapedial pattern, continues rostrally in a shallow groove along the inner surfaces of the squamosal and alisphenoid bones (fig. 23, **gr**). Where this interior, longitudinal groove (often visible as a streak of translucent bone) crosses the external, vertical trough marked by the passage of the buccinator and masticatory nerves (fig. 23, **bmt**), a small hole is often eroded through the lateral wall of the braincase; the supraorbital branch exits the braincase and enters the orbital fossa through the sphenofrontal foramen (fig. 23, **sf**). The infraorbital branch

passes ventrally along the anterior margin of the bulla to enter the alisphenoid canal through the foramen ovale or by a separate posterior opening. Rostrally, the course of the infraorbital branch is not well defined by bony structures and may occasionally be extracranial; in most specimens, however, the vessel apparently enters the orbit through the anterior alar fissure. In specimens with an incomplete stapedial circulation (pattern 2 of Voss, 1988), the stapedial artery is undivided and follows the course described above for the infraorbital branch; the squamosal-alisphenoid groove and the sphenofrontal foramen are therefore absent. In a few specimens, both patterns of stapedial circulation are present on opposite sides of the skull.

Frequencies of these two stapedial arterial patterns distinguish a northwestern and a southeastern series of populations (table 10). The northwestern series includes all of the available samples from Central America, northern Colombia, the upper Magdalena valley, the Maracaibo basin, and the western Caribbean coast of Venezuela; these are characterized by high frequencies (86 to 100%) of specimens with complete stapedial circulations. Specimens from southeastern populations, however, usually lack a supraorbital branch of the stapedial artery; included are

TABLE 10
Frequencies of Alternative Stapedial Circulation
Patterns in Population Samples of
Zygodontomys brevicauda

Populations ^a	N	Stapedial circulation ^b		
		1-1	1-2	2-2
Northwestern Series				
Costa Rica				
3. Finca Helechales	28	0.86	0.11	0.04
Panama				
12. Rodman Naval A.D.	38	0.90	0.03	0.08
26. Cerro Azul	63	0.97	0.02	0.02
28. San Miguel Island	49	0.86	0.08	0.06
30. Armila Village	26	0.96	0.04	0.00
31. Isla Cébaco	126	0.99	0.01	0.00
32. Montijo Bay	51	0.92	0.06	0.02
Colombia				
16. Montería	20	0.95	0.00	0.01
20. Villanueva	64	0.98	0.00	0.02
Venezuela				
13. Ocumare de la Costa	22	1.00	0.00	0.00
37. Urama	43	0.86	0.05	0.09
41. Hacienda Socopito	33	0.94	0.06	0.00
49. El Tocuyo	20	0.90	0.00	0.10
72. El Dividive	99	0.98	0.02	0.00
79. Misión Tukuko	39	0.97	0.03	0.00
Southeastern Series				
Colombia				
32. Villavicencio	25	0.00	0.00	1.00
Venezuela				
2. Belén	42	0.05	0.10	0.86
3. Esmeralda	57	0.14	0.25	0.61
4. San Juan Manapiare	52	0.12	0.19	0.69
8. Hato El Frío	51	0.04	0.02	0.94
19. Auyátepui	49	0.00	0.00	1.00
30. Roraima	36	0.06	0.03	0.92
32. San Ignacio Yuruani	33	0.00	0.03	0.97
48. Parcela 200	34	0.08	0.06	0.85
54. Río Chico	42	0.00	0.14	0.86
59. Hato Mata de Bejuco	32	0.00	0.09	0.91
60. San Antonio Maturín	21	0.00	0.00	1.00
69. Finca Vuelta Larga	33	0.06	0.06	0.88
Trinidad and Tobago				
1-5. Tobago	63	0.02	0.03	0.95
6. Bush Bush Forest	46	0.00	0.04	0.96
9. Sangre Grande	56	0.00	0.02	0.98
Brazil				
3. Limão	67	0.02	0.02	0.97
Surinam				
11. Paramaribo	39	0.00	0.00	1.00
French Guiana				
2. Cacao	20	0.10	0.00	0.90
3. Cayenne	21	0.00	0.10	0.90

samples from eastern Colombia, the entire Orinoco basin, the eastern Caribbean coast of Venezuela, the upper Rio Branco drainage of Brazil, and coastal areas of the Guianas. These distributions apparently reflect divergence in allopatry because the northwestern and southeastern series of populations are ecogeographically separated (fig. 24). The Andean Cordillera Oriental, the Cordillera de Merida, and the Cordillera de la Costa form an arc of montane habitats interrupted by lowland gaps that were forested within historic times. Since *Zygodontomys* is restricted to nonforest lowland vegetation (see Natural History, below), gene flow was presumably negligible across this mountain-forest barrier until the advent of recent deforestation.

In most populations of *Z. brevicauda*, the bony roof of the mesopterygoid fossa is fenestrated by large sphenopalatine vacuities (fig. 25, left, spv) that flank the basisphenoid/presphenoid suture, reducing the basicranial axis to a median bridge of bone. From Costa Rica to southern Guyana, sphenopalatine vacuities occur in nearly 100 percent of the specimens examined (table 11). By contrast, specimens from northern Guyana, northern Surinam, and French Guiana lack large sphenopalatine vacuities (table 11); the mesopterygoid fossa in these is usually completely roofed with bone (fig. 25, right) but small, irregular slits are sometimes present on either side of the basisphenoid/presphenoid suture.

Substantial morphometric divergence is also evident among populations of *Zygodontomys brevicauda*. Twenty or more specimens with complete craniodental measurement data are available from 29 populations (table 12), but cluster analyses and ordinations that include all of these samples reveal few comprehensible patterns. In the example illustrated (fig. 26), a few clusters suggest that phenotypic similarity and geographic distance are

^a Numbered and named as in Materials and Methods.

^b Key: 1-1, complete stapedial circulation on both sides of skull; 1-2, complete and incomplete stapedial circulations on opposite sides of skull; 2-2, incomplete stapedial circulation on both sides of skull.

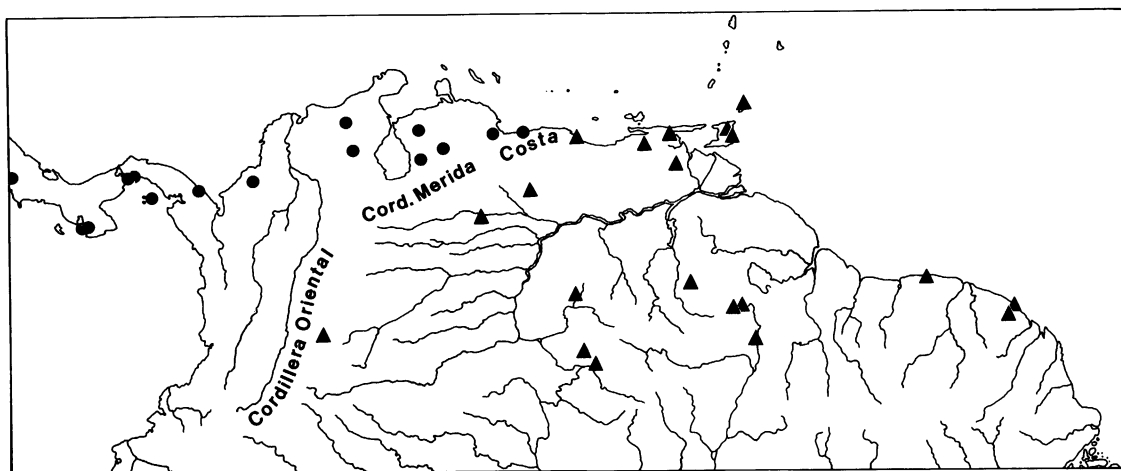


Fig. 24. Geographic pattern of stapedial arterial frequencies. (●) The northwestern series of populations with high frequencies of complete stapedial circulations; (▲) southeastern populations with high frequencies of incomplete stapedial circulations (see table 10).

correlated (an observation consistent with simple scenarios of faunal dispersion and contemporary gene flow), but the majority are too geographically heterogeneous to support any reasonable historical interpretation. Since, additionally, it is impossible to distinguish primitive and derived similarity in these results, morphometric comparisons are reserved for consideration within geographic units of *Z. brevicauda* defined by other (qualitative) characters.

REMARKS: Subspecific nomenclature is employed below to identify allopatric groups of populations that appear to represent phylo-

genetic units of zoogeographic significance. Clearly, the utility of subspecific taxa so recognized will depend on their genetic distinctness and the historical interest of the areas they occupy. Equally obvious is that such entities could as well be called species unless some additional biological properties or more stringent recognition criteria are reserved for the latter category.

I reserve species rank for diagnosable and reproductively isolated groups of populations. *Zygodontomys brevicauda* and *Z. brunneus*, for example, are each diagnosable and their reproductive isolation is docu-

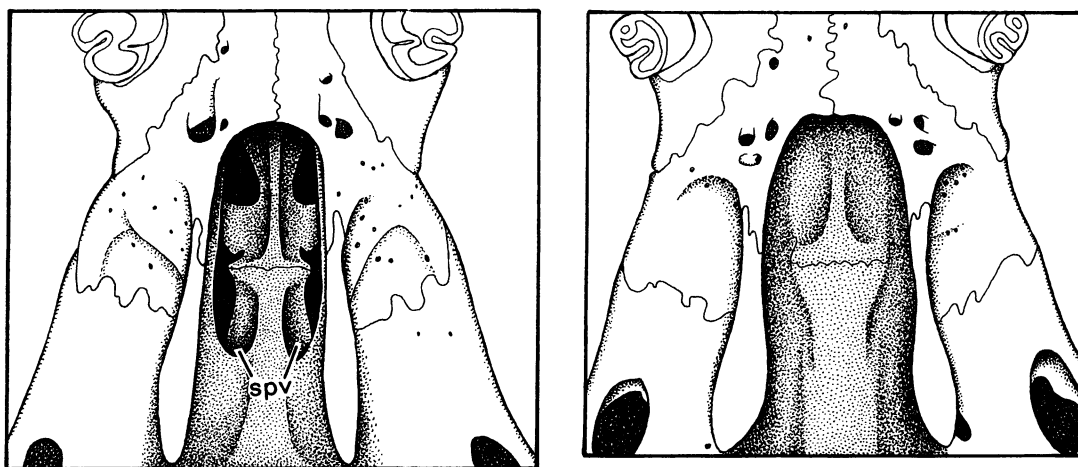


Fig. 25. Mesopterygoid fossae. Left, *Zygodontomys brevicauda brevicauda* (MHNLS 8153); right, *Z. b. microtinus* (RMNH 18260D.) spv, sphenoplatine vacuities.

TABLE 11
Frequency of Occurrence of Sphenopalatine
Vacuities in Population Samples of
Zygodontomys brevicauda

Populations ^a	N	Present	Absent
Costa Rica			
3. Finca Helechales	28	1.00	0.00
Panama			
26. Cerro Azul	64	1.00	0.00
31. Isla Cébaco	75	1.00	0.00
32. Montijo Bay	48	1.00	0.00
Colombia			
20. Villanueva	94	1.00	0.00
Venezuela			
2. Belén	30	1.00	0.00
8. Hato El Frío	42	1.00	0.00
32. San Ignacio Yuruaní	27	0.96	0.04 ^b
69. Finca Vuelta Larga	33	1.00	0.00
72. El Dividive	62	1.00	0.00
Trinidad and Tobago			
1. Charlotteville	29	1.00	0.00
Brazil			
3. Limão	66	1.00	0.00
Surinam			
11. Paramaribo	26	0.15 ^c	0.85
French Guiana			
2. Cacao	22	0.09 ^c	0.91
3. Cayenne	21	0.19 ^c	0.81

^a Numbered and named as in Materials and Methods.

^b One very old adult.

^c Specimens scored for presence in these populations exhibit very small slits that are unlike the widely open sphenopalatine vacuities of other populations.

mented by sympatry in the upper Magdalena valley of Colombia. The use of trinomials to describe groups of populations within *Z. brevicauda* then serves to emphasize their similarities *inter se* while drawing attention to patterns of geographic variation that may have phylogenetic explanations. Finally, it can be argued that groups of populations distinguished by trait frequency differences should not be treated as species since individual specimens exhibit traits, not frequencies, and therefore can only be identified by their membership in samples.

ZYGODONTOMYS BREVICAUDA BREVICAUDA

(J. A. Allen and Chapman)

Oryzomys brevicauda Allen and Chapman, 1893: 215.

Akodon frustrator Allen and Chapman, 1897: 20.

TABLE 12
Population Samples of *Zygodontomys brevicauda*
Included in Morphometric Analyses
(Descriptive sample statistics, including the mean, standard deviation, and observed range, are provided in tables accompanying the subspecies accounts.)

Populations ^a	N
Costa Rica	
3. Finca Helechales	20
Panama	
26. Cerro Azul	38
28. San Miguel Island	39
31. Isla Cébaco	51
32. Montijo Bay	33
Colombia	
20. Villanueva	29
32. Villavicencio	23
Venezuela	
2. Belén	20
3. Esmeralda	28
4. San Juan Manapiare	21
8. Hato El Frío	48
19. Auyántepeui	23
30. Roraima	20
32. San Ignacio Yuruaní	25
37. Urama	30
41. Hacienda Socopito	22
48. Parcela 200	29
54. Río Chico	33
60. San Antonio Maturín	20
69. Finca Vuelta Larga	30
72. El Dividive	68
79. Misión Tukuko	36
Trinidad and Tobago	
1. Charlotteville	25
6. Bush Bush Forest	30
9. Sangre Grande	27
Brazil	
3. Limão	37
Surinam	
11. Paramaribo	27
French Guiana	
2. Cacao	23
3. Cayenne	21

^a Named and numbered as in Materials and Methods.

Zygodontomys brevicauda Allen, 1897: 38.

Zygodontomys stellae Thomas, 1899: 380.

Zygodontomys brevicauda tobagi Thomas, 1900: 274.

Zygodontomys thomasi Allen, 1901: 39.

Zygodontomys brevicauda brevicauda Gyldenstolpe, 1932: 112.

Zygodontomys microtinus stellae Tate, 1939: 188.

Zygodontomys punctulatus thomasi Cabrera, 1961: 465.

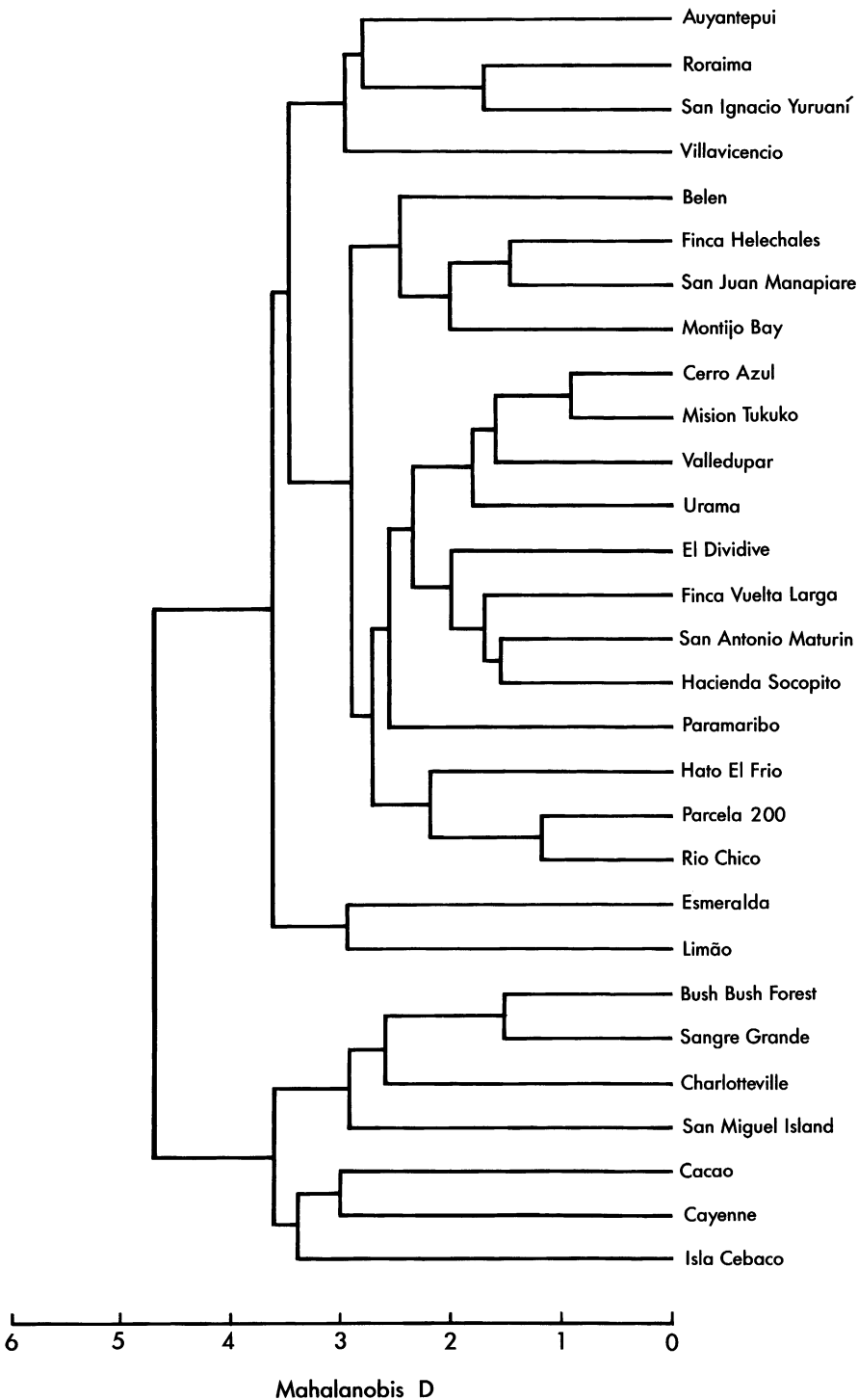


Fig. 26. UPGMA clustering of Mahalanobis distances (D) among the 29 population samples of *Zygodontomys brevicauda* listed in table 12.

Zygodontomys brevicauda stellae Hershkovitz, 1962: 205.

Zygodontomys brevicauda thomasi Hershkovitz, 1962: 205.

Zygodontomys brevicauda soldadoensis Goodwin, 1965: 2.

Zygodontomys microtinus thomasi Reig, 1986: 407.

TYPE MATERIAL: As for the species.

DISTRIBUTION: On the South American mainland, from the headwaters of the Río Guaviare in eastern Colombia throughout the Llanos and other unforested landscapes of the Orinoco basin; the Caribbean coast of Venezuela from the valley of the Río Tuy east to the Paria Peninsula; the savannas of the upper Rio Branco in Brazil; and the Rupununi savannas of interior Guyana. Populations referred to this subspecies also occur on adjacent islands of the continental shelf, including Isla Margarita, Trinidad (the type locality), and Tobago.

MORPHOLOGICAL CHARACTERS AND COMPARISONS: Populations of *Zygodontomys brevicauda brevicauda* are distinguished from those of other subspecies by the predominance of incomplete stapedial circulations and by the fenestrated morphology of the mesopterygoid fossa (see the preceding discussion of these characters under Geographic Variation in the species account for *Z. brevicauda*, above). Complete stapedial circulations predominate in populations of *Z. b. cherriei* and an unfenestrated mesopterygoid fossa characterizes *Z. b. microtinus*.

KARYOTYPES: Karyotypic data for *Zygodontomys brevicauda brevicauda* were provided by Kiblinki et al. (1970), Gardner and Patton (1976), Perez-Zapata et al. (1984), and Reig et al. (1990). Diploid numbers range from 84 to 88 chromosomes, and fundamental numbers (of autosomal arms) range from 116 to 118. Much of the genome appears to be heterochromatic. Reig et al. (1990) included photographs of standard (nondifferentially stained) and C-banded karyotypes in their report.

GEOGRAPHIC VARIATION: Variation among population samples of *Zygodontomys brevicauda brevicauda* is evident in pelage color and craniodental dimensions. The extremes of pelage color within the subspecies are rep-

resented on the one hand by dark, richly pigmented skins from Trinidad and Tobago, and on the other by pale, grayish-sandy skins from the savannas of interior Guyana and the adjacent upper Rio Branco drainage of Brazil. Other populations present a continuous array of intermediate hues with no evidence of well defined regional differentiation worthy of formal recognition.

Morphometric variation in skulls and teeth provides some evidence of geographic patterns (fig. 27). Most divergent is a cluster of samples from Trinidad (Bush Bush Forest and Sangre Grande) and Tobago (Charlotteville) that differ from mainland samples by an average Mahalanobis distance (D) of about 4.9 (see Materials and Methods for an explanation of this statistic). Craniodental dimensions of island specimens (table 13) average substantially larger than those of specimens from adjacent mainland populations (table 14).

Among mainland samples, only a single cluster of five populations from north-central Venezuela appears to exhibit substantial divergence from the rest: Hato El Frío (Venezuelan locality 8), Parcela 200 (locality 48), Río Chico (locality 54), San Antonio Maturín (locality 60), and Finca Vuelta Larga (locality 69). These populations represent a region of continuous habitat across the Llanos and adjoining deforested areas north of the Orinoco; no geographical barriers to gene exchange occur within this region, and the samples exhibit remarkable morphometric uniformity (table 14).

Mahalanobis distances among the remaining mainland population samples of *Z. b. brevicauda* (with descriptive statistics in tables 15 and 16) exhibit no significant hierarchical structure: most cluster over a narrow range of fairly high D-values with the exception of a pair (Roraima and San Ignacio Yuruaní; Venezuelan localities 30 and 32) from collection sites only 40 km apart. Villavicencio (Colombian locality 32) is in the extreme western Llanos near the base of the Andes, but the other samples represent an archipelago of savanna habitats widely scattered across the rain forests of southern Venezuela, northern Brazil, and interior Guyana. The absence of well defined geographic patterns

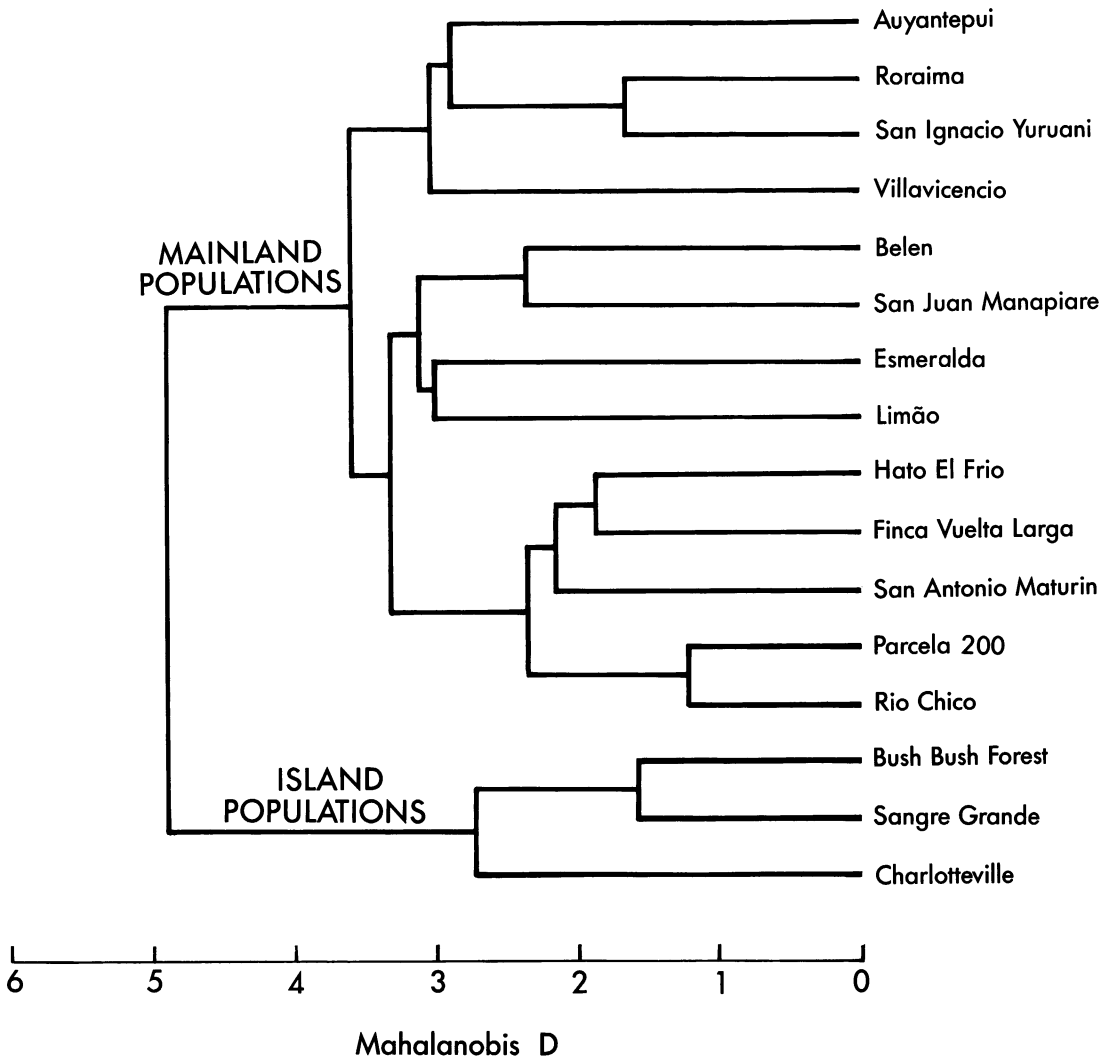


Fig. 27. UPGMA clustering of Mahalanobis distances (D) among 16 population samples of *Zygodontomys brevicauda brevicauda*. Sample sizes and geographical information are provided in table 12.

of phenotypic similarity among these samples perhaps reflects their genetic isolation (see Biogeography, below) and the consequences of stochastic processes of population divergence.

Principal components analysis (fig. 28, table 17) essentially corroborates the observations based on UPGMA clustering of Mahalanobis distances. Two orthogonal axes account for almost 90 percent of the morphometric variation among sample means. The first component, with coefficients reflecting joint increase of all measured dimensions,

accounts for most of the differentiation between island and mainland samples, while the second separates the discrete cluster of north-central Venezuelan samples identified above from the more diffuse array of other mainland localities. Inspection of the coefficients of PC2 (table 17, second column) suggests that Venezuelan populations north and south of the Orinoco are distinguished chiefly by palatal breadth (BPB). An impression of the magnitude of this difference can be obtained by inspection of mean values for the Hato El Frio and San Ignacio Yuruaní sam-

TABLE 13
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brevicauda brevicauda* from Trinidad and Tobago

	Trinidad		Tobago
	Bush Bush Forest ^b (18 ♂, 10 ♀, 2 unk.)	Sangre Grande ^c (14 ♂, 12 ♀, 1 unk.)	Charlotteville ^d (11 ♂, 11 ♀, 3 unk.)
CIL	27.8 ± 1.63 (23.9–29.8)	27.5 ± 1.50 (24.1–30.0)	29.2 ± 2.50 (24.6–33.6)
LD	8.1 ± 0.68 (6.4–9.0)	8.0 ± 0.58 (6.8–9.0)	8.5 ± 1.04 (6.7–10.1)
LM	4.6 ± 0.16 (4.3–5.0)	4.6 ± 0.15 (4.3–5.0)	4.7 ± 0.16 (4.4–5.1)
BM1	1.4 ± 0.04 (1.4–1.5)	1.4 ± 0.06 (1.3–1.6)	1.5 ± 0.07 (1.4–1.6)
LIF	6.5 ± 0.41 (5.4–7.2)	6.2 ± 0.38 (5.4–7.0)	7.0 ± 0.74 (5.6–8.6)
BR	4.9 ± 0.34 (4.1–5.4)	4.9 ± 0.30 (4.3–5.5)	5.2 ± 0.59 (4.1–6.4)
BPB	3.0 ± 0.26 (2.4–3.4)	3.0 ± 0.29 (2.3–3.4)	3.1 ± 0.46 (2.4–4.2)
BZP	3.0 ± 0.28 (2.4–3.5)	3.1 ± 0.33 (2.4–3.6)	3.3 ± 0.37 (2.4–4.0)
LIB	4.8 ± 0.23 (4.2–5.4)	4.9 ± 0.22 (4.5–5.4)	5.2 ± 0.26 (4.6–5.7)
BB	12.4 ± 0.36 (11.6–13.0)	12.4 ± 0.37 (12.0–13.6)	12.8 ± 0.50 (11.2–13.8)
DI	1.6 ± 0.11 (1.4–1.8)	1.6 ± 0.12 (1.3–1.8)	1.7 ± 0.20 (1.4–2.0)
LOF	10.3 ± 0.58 (9.1–11.4)	10.3 ± 0.57 (9.2–11.2)	10.5 ± 0.78 (9.1–12.2)

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

^b Trinidad and Tobago locality 6.

^c Trinidad and Tobago locality 9.

^d Trinidad and Tobago locality 1.

ples (tables 14 and 16, respectively); specimens from these populations are closely comparable in size (as evidenced by similar scores on PC1 and similar means for CIL), but differ by about 0.3 mm (on average) in palatal breadth, a contrast that is also discernable by visual comparisons of large series of skulls. Subsequent components, each accounting for 6 percent or less of the total variance, provide no additional insights.

Close study of large numbers of specimens reveals no consistent regional differentiation among populations of *Z. b. brevicauda* in qualitative features of the skin, skull, or dentition. Except for the pelage color and morphometric variation described above, these samples present a uniform aspect consistent with their proposed membership in a single taxon.

REMARKS: The ranges of *Zygodontomys brevicauda brevicauda* and *Z. b. microtinus* converge in Guyana where the former is apparently restricted to the interior savannas of the Rupununi district and the latter to the coastal savannas east of the Essequibo. In addition to the cited subspecific distinction of mesopterygoid fenestration, Guyanese *microtinus* and *brevicauda* differ in size and pelage color. The few available specimens of *mi-*

crotinus from Guyana are larger animals with dark, indistinctly countershaded pelts, while Rupununi samples of *brevicauda* are smaller and pale, with whitish underparts. As a rough indication of the cited size difference, hindfeet of adult Rupununi *brevicauda* range from 21 to 24 mm while the single measurable hindfoot of an adult *microtinus* from Guyana is 28 mm. Additional Guyanese collections of both subspecies are required to test these characterizations as well as to determine the geographic limits of the two phenotypes.

SPECIMENS EXAMINED: **Brazil**—*Roraima*, Frechal (AMNH 2), Limão (AMNH 67), Serra de Lua (BMNH 4, FMNH 5). **Colombia**—*Casanare*, Finca Balmoral (UVM 19); *Meta*, Fuente de Oro (ICN 1), Puerto Gaitán (UVM 7), Puerto Lopez (ICN 6), Puerto Lleras (ICN 1), Restrepo (AMNH 1), San Juan de Arama (FMNH 10, UVM 10), San Martín (ICN 1), Villavicencio (AMNH 17, MVZ 1, ROM 3, USNM 8); *Vichada*, Maipures (BMNH 2, including the type of *stellae*), Puerto Carreño (UVM 12), Territorio Faunístico “El Tuparro” (CMIND 3). **Guyana**—*Rupununi*, Dadanawa (ROM 6), Kanuku Mountains (BMNH 12, FMNH 2), Nappi Creek (ROM 25), Weri More (ROM 5). **Trinidad and Tobago**—*Tobago*, Charlotteville (AMNH 28,

TABLE 14
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brevicauda* from Venezuelan Localities North of the Orinoco River

	Hato El Frío ^b (28 ♂, 20 ♀)	Parcela 200 ^c (14 ♂, 11 ♀, 4 unk.)	Río Chico ^d (19 ♂, 14 ♀)	San Antonio M. ^e (11 ♂, 9 ♀)	Finca Vuelta Larga ^f (18 ♂, 12 ♀)
CIL	26.0 ± 1.59 (22.8–28.8)	26.2 ± 1.61 (22.9–29.3)	25.7 ± 2.05 (21.4–29.5)	25.9 ± 1.31 (23.6–28.0)	26.6 ± 1.82 (23.2–30.6)
LD	7.4 ± 0.66 (6.1–8.3)	7.4 ± 0.61 (6.2–8.5)	7.2 ± 0.74 (5.8–8.5)	7.1 ± 0.50 (6.3–8.0)	7.5 ± 0.70 (6.4–9.1)
LM	4.2 ± 0.17 (3.8–4.6)	4.1 ± 0.16 (3.8–4.5)	4.1 ± 0.20 (3.8–4.6)	4.3 ± 0.19 (3.9–4.6)	4.3 ± 0.16 (4.0–4.6)
BM1	1.3 ± 0.06 (1.2–1.4)	1.3 ± 0.05 (1.2–1.4)	1.2 ± 0.06 (1.1–1.4)	1.3 ± 0.05 (1.2–1.4)	1.4 ± 0.05 (1.2–1.5)
LIF	6.1 ± 0.42 (5.1–6.8)	6.1 ± 0.50 (5.2–7.1)	6.0 ± 0.55 (4.6–7.0)	5.8 ± 0.31 (5.2–6.3)	6.1 ± 0.48 (5.2–7.1)
BR	4.7 ± 0.33 (4.0–5.4)	4.7 ± 0.38 (4.0–5.2)	4.6 ± 0.38 (3.9–5.4)	4.7 ± 0.30 (4.2–5.2)	4.7 ± 0.38 (4.0–5.5)
BPB	2.7 ± 0.30 (2.2–3.2)	2.8 ± 0.25 (2.4–3.3)	2.7 ± 0.28 (2.0–3.1)	2.8 ± 0.31 (2.2–3.3)	2.8 ± 0.33 (2.4–3.8)
BZP	2.9 ± 0.31 (2.2–3.4)	3.0 ± 0.31 (2.4–3.6)	2.9 ± 0.38 (2.2–3.7)	2.9 ± 0.34 (2.3–3.6)	3.0 ± 0.38 (2.4–3.6)
LIB	4.4 ± 0.18 (4.1–4.8)	4.5 ± 0.22 (4.1–4.9)	4.5 ± 0.19 (4.1–4.8)	4.5 ± 0.13 (4.3–4.8)	4.6 ± 0.23 (4.0–5.0)
BB	11.6 ± 0.40 (10.8–12.5)	11.7 ± 0.40 (10.8–12.6)	11.5 ± 0.47 (10.8–12.4)	11.8 ± 0.35 (11.3–12.5)	11.9 ± 0.35 (11.2–12.7)
DI	1.4 ± 0.13 (1.2–1.7)	1.5 ± 0.14 (1.2–1.8)	1.5 ± 0.17 (1.2–1.8)	1.5 ± 0.12 (1.2–1.8)	1.5 ± 0.13 (1.2–1.9)
LOF	9.9 ± 0.56 (8.7–11.0)	10.0 ± 0.53 (9.0–11.0)	9.7 ± 0.73 (8.1–11.1)	9.8 ± 0.51 (9.0–10.6)	10.0 ± 0.58 (8.7–11.3)

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

^b Venezuelan locality 8.

^c Venezuelan locality 48.

^d Venezuelan locality 54.

^e Venezuelan locality 60.

^f Venezuelan locality 69.

TABLE 15
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brevicauda brevicauda* from eastern Colombia and Southern Venezuela

	Villavicencio ^b (17 ♂, 6 ♀)	San Juan M. ^c (14 ♂, 7 ♀)	Belén ^d (4 ♂, 16 ♀)	Esmeralda ^e (14 ♂, 12 ♀, 2 unk.)
CIL	27.9 ± 1.19 (25.6–30.6)	27.1 ± 1.57 (22.6–29.8)	25.6 ± 1.40 (22.0–28.2)	25.4 ± 1.25 (22.6–28.2)
LD	7.8 ± 0.48 (7.0–8.8)	7.7 ± 0.57 (6.1–8.7)	7.2 ± 0.52 (6.0–8.1)	7.2 ± 0.41 (6.2–8.0)
LM	4.4 ± 0.17 (4.0–4.6)	4.2 ± 0.20 (3.7–4.6)	4.0 ± 0.12 (3.8–4.2)	4.0 ± 0.14 (3.8–4.3)
BM1	1.4 ± 0.07 (1.3–1.6)	1.3 ± 0.05 (1.2–1.4)	1.3 ± 0.05 (1.2–1.4)	1.2 ± 0.04 (1.2–1.3)
LIF	6.6 ± 0.35 (5.9–7.2)	6.1 ± 0.38 (5.2–7.0)	5.8 ± 0.35 (5.0–6.5)	5.6 ± 0.29 (5.0–6.2)
BPB	3.2 ± 0.23 (2.7–3.6)	3.0 ± 0.22 (2.6–3.3)	3.0 ± 0.29 (2.4–3.6)	3.0 ± 0.22 (2.6–3.5)
BZP	3.0 ± 0.27 (2.4–3.4)	2.9 ± 0.32 (2.2–3.4)	2.6 ± 0.25 (1.8–2.9)	2.7 ± 0.23 (2.2–3.2)
LIB	4.9 ± 0.24 (4.4–5.4)	4.8 ± 0.27 (4.4–5.4)	4.6 ± 0.15 (4.3–5.0)	4.5 ± 0.15 (4.3–4.8)
BB	12.2 ± 0.34 (11.4–13.0)	11.9 ± 0.42 (11.2–12.8)	11.7 ± 0.28 (11.1–12.2)	11.8 ± 0.34 (11.2–12.4)
DI	1.5 ± 0.12 (1.3–1.8)	1.5 ± 0.13 (1.2–1.8)	1.4 ± 0.10 (1.2–1.6)	1.5 ± 0.12 (1.3–1.8)
LOF	10.5 ± 0.41 (9.8–11.5)	10.3 ± 0.51 (9.0–11.3)	9.7 ± 0.52 (8.6–10.6)	9.5 ± 0.41 (8.4–10.3)

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

^b Colombian locality 32.

^c Venezuelan locality 4.

^d Venezuelan locality 2.

^e Venezuelan locality 3.

USNM 35), Lambeau Hill Crown Trace and Windward Road (USNM 2), Richmond (BMNH 2, including the type of *tobagi*), Roxborough (USNM 3), Speyside (AMNH 11); *Trinidad*, Bush Bush Forest (AMNH 46), Caparo (AMNH 5), Caura (AMNH 17, including the type of *frustrator*), Sangre Grande

(AMNH 56), North Manzanilla (AMNH 1), Princetown (AMNH 18, including the type of *brevicauda*), Soldado Rock (AMNH 21, including the type of *soldadoensis*). *Venezuela—Amazonas*, Atures (MARNR 1), Belén (USNM 42), Esmeralda (AMNH 17, MBUCV 26), San Juan Manapiare (USNM 52); *An-*

TABLE 16
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brevicauda brevicauda* from Southeastern Venezuela and Northern Brazil

	Auyántepui ^b (12 ♂, 11 ♀)	San Ignacio Y. ^c (15 ♂, 10 ♀)	Roraima ^d (10 ♂, 10 ♀)	Limão ^e (23 ♂, 14 ♀)
CIL	27.2 ± 1.21 (25.4–30.0)	25.9 ± 1.34 (23.4–28.4)	24.8 ± 1.61 (21.6–27.6)	24.5 ± 1.19 (21.0–27.3)
LD	7.7 ± 0.45 (7.0–8.7)	7.3 ± 0.59 (6.2–8.4)	6.9 ± 0.61 (5.8–7.8)	6.9 ± 0.41 (5.7–7.9)
LM	4.3 ± 0.15 (4.0–4.7)	4.3 ± 0.17 (4.0–4.8)	4.3 ± 0.17 (3.8–4.5)	3.9 ± 0.16 (3.6–4.2)
BM1	1.3 ± 0.04 (1.2–1.4)	1.3 ± 0.07 (1.2–1.4)	1.3 ± 0.06 (1.2–1.4)	1.2 ± 0.04 (1.2–1.3)
LIF	6.1 ± 0.35 (5.4–7.0)	6.2 ± 0.45 (5.2–6.9)	6.0 ± 0.51 (4.9–7.0)	5.7 ± 0.35 (4.7–6.3)
BR	5.0 ± 0.27 (4.6–5.6)	4.6 ± 0.30 (4.0–5.2)	4.5 ± 0.29 (4.0–5.0)	4.4 ± 0.26 (3.7–4.8)
BPB	3.3 ± 0.25 (2.8–3.8)	3.0 ± 0.29 (2.4–3.4)	3.0 ± 0.31 (2.6–3.6)	2.8 ± 0.26 (1.8–3.2)
BZP	3.2 ± 0.21 (2.7–3.5)	2.8 ± 0.25 (2.4–3.2)	2.6 ± 0.24 (2.2–3.0)	2.6 ± 0.25 (2.0–3.2)
LIB	4.7 ± 0.17 (4.5–5.0)	4.6 ± 0.20 (4.2–4.8)	4.5 ± 0.16 (4.2–4.9)	4.3 ± 0.19 (3.9–4.7)
BB	12.1 ± 0.27 (11.5–12.6)	11.8 ± 0.32 (11.0–12.3)	11.5 ± 0.42 (10.4–12.4)	11.2 ± 0.33 (10.1–11.8)
DI	1.5 ± 0.09 (1.4–1.7)	1.4 ± 0.13 (1.2–1.6)	1.4 ± 0.12 (1.2–1.6)	1.4 ± 0.09 (1.2–1.6)
LOF	10.3 ± 0.46 (9.6–11.4)	9.7 ± 0.43 (8.9–10.6)	9.4 ± 0.63 (8.0–10.7)	9.4 ± 0.42 (8.2–10.3)

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

^b Venezuelan locality 19.

^c Venezuelan locality 32.

^d Venezuelan locality 30.

^e Brazilian locality 3.

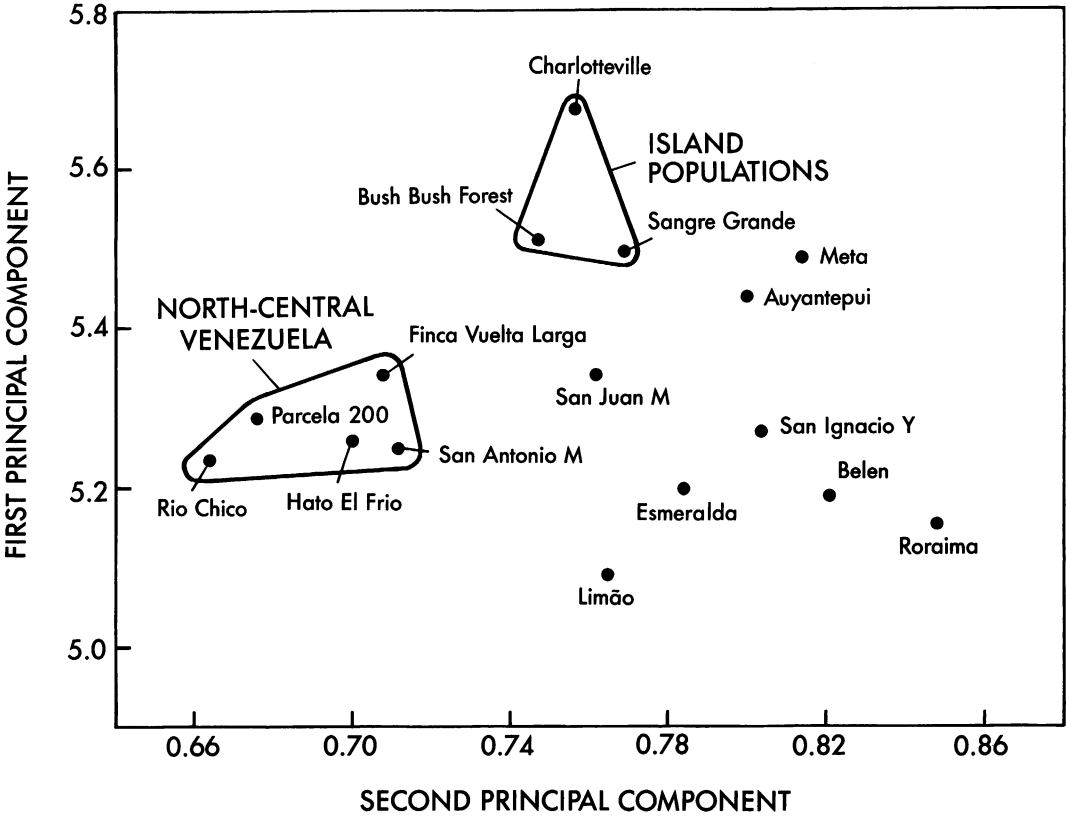


Fig. 28. Principal components analysis of 16 population samples of *Zygodontomys brevicauda brevicauda*. Components were extracted from the covariance matrix of log-transformed sample means; eigenvalues (expressed as percentages) and eigenvector coefficients are provided in table 17. Sample sizes and geographic information are provided in table 12.

zoátegui, Mamo (MHNLS 7), Río Caris (MBUCV 5), Río Pao (MBUCV 2); *Apure*, “Caño La Guardia” (MHNLS 5), Hato El Frio (MHNLS and USNM 51), Hato La Trinidad de Arauca (MBUCV 6), 41 km NW Puerto Paez (USNM 9), 60 km NE Puerto Paez (USNM 3), 95–115 km NW Puerto Paez (USNM 1); *Aragua*, Campo Rangel (USNM 5); *Barinas*, Barrancas (CVULA 6), Hato La Candelaria (CVULA 1), Santa Barbara (MARNR 1), Ticoporo (CVULA 1); *Bolívar*, Auyantepui (AMNH 52), Boca de Parguaza (MBUCV 2), Camp Mop (MBUCV 1), Churitepui (AMNH 1), 29 km WSW Ciudad Bolívar (MBUCV 1), El Llual (AMNH 5), Represa de Guri (MBUCV 1), Hato La Florida (USNM 18), Hato San José (USNM 5), 46–54 km NE Icabarú (USNM 4), Cumbre del Abismo (MHNLS 1), Morichal Aguas Negras

(MHNLS 1), Kavanayén (AMNH 2), Roraima (AMNH 36), “Rumon” (AMNH 1), Salto Uraima (MBUCV 1), San Ignacio Yuruaní (AMNH, MHNLS, and USNM 27), San Martín de Turumbán (MHNLS 4); *Cojedes*, Hato Itabana (MHNLS 8), Hato Los Caballos (MHNLS 4), Hato Nuevo (MARNR 6); *Guárico*, Estación Biológica de los Llanos (UCV and USB 15), Hato La Fe (MHNLS 4), Hato Las Palmitas (USNM 11), Hato Los Leones (USNM 2), Hato Mata de Bejuco (MBUCV 1), Parcela 200 (MHNLS 34); *Miranda*, 19 km E Caracas (USNM 1), Río Chico (USNM 43); *Monagas*, Caripe (MBUCV 8, USNM 7), 20 km SE Chaguaramas (MHNLS 1), Guana Guana (MBUCV 1), Isla Guara (USB 3), Hato Mata de Bejuco (USNM 28), Río Cocollar (AMNH 3), San Antonio de Maturín (AMNH 21); *Nueva Esparta*, Cerro Ma-

tasiete (USNM 2); *Portuguesa*, Acarigua (CVULA 1), Colegio Agrícola Turén (CVULA 2), Tierra Buena (USB 1); *Sucre*, Campo Alegre (BMNH 2, including the type of *thomasi*), Cristobal Colón (AMNH 6), Cuchivano (AMNH 1), Cumaná (USNM 8), Cumanacoa (AMNH 12), Ensenada Cauranta (USNM 15), Finca Vuelta Larga (AMNH and MHNLS 33), "near Guacuco" (MHNLS 4), Manacal (USNM 12), Quebrada Seca (AMNH 1), "Serranía de Marigüitar" (MBUCV 1); *Táchira*, Estación Experimental (CVULA 1). TOTAL = 1160.

ZYGODONTOMYS BREVICAUDA
CHERRIEI (J. A. Allen)

- Oryzomys cherriei* Allen, 1895: 329.
Zygodontomys cherriei Allen, 1897: 38.
Oryzomys sanctaemartae Allen, 1899: 207.
Zygodontomys seorsus Bangs, 1901: 642.
Zygodontomys cherriei ventriosus Goldman, 1912: 8.
Zygodontomys thomasi sanctaemartae Osgood, 1912: 52.
Zygodontomys griseus Allen, 1913: 599.
Zygodontomys fraterculus Allen, 1913: 599.
Zygodontomys sanctaemartae Gyldenstolpe, 1932: 113.
Zygodontomys cherriei cherriei Ellerman, 1941: 418.
Zygodontomys microtinus fraterculus Cabrera, 1961: 464.
Zygodontomys punctulatus griseus Cabrera, 1961: 464.
Zygodontomys punctulatus sanctaemartae, Cabrera, 1961: 464.
Zygodontomys brevicauda cherriei, Hershkovitz, 1962: 203.
Zygodontomys brevicauda ventriosus, Hershkovitz, 1962: 204.
Zygodontomys brevicauda seorsus, Hershkovitz, 1962: 204.
Zygodontomys brevicauda sanctaemartae, Hershkovitz, 1962: 204.

TYPE MATERIAL: As described earlier for the genus.

DISTRIBUTION: On the Central and South American mainland, from the Pacific littoral of eastern Costa Rica throughout Panama, the Caribbean lowlands of Colombia, the upper Magdalena valley, and the Maracaibo basin and Caribbean coast of Venezuela east to about the latitude of Lago de Valencia. This subspecies also occurs on adjacent continen-

TABLE 17
Results of Principal Components Analysis of Craniodental Measurement Means From 16 Population Samples of *Zygodontomys brevicauda brevicauda*

(See Materials and Methods, accompanying text, and figure 28.)

	First principal component	Second principal component
% Variance	77.5	9.2
Coefficients:		
CIL	0.29	-0.03
LD	0.36	0.00
LM	0.29	0.10
BM1	0.29	0.15
LIF	0.31	0.01
BR	0.28	-0.00
BPB	0.19	0.77
BZP	0.40	-0.45
LIB	0.26	0.23
BB	0.20	0.06
DI	0.30	-0.34
LOF	0.22	-0.03

tal-shelf islands, including Isla Cébaco and the Pearl Archipelago of Panama.

MORPHOLOGICAL CHARACTERS AND COMPARISONS: Populations of *Zygodontomys brevicauda cherriei* are distinguished from those of other subspecies by the predominance of complete stapediaal arterial circulations and by the presence of large sphenopalatine vacuities in the roof of the mesopterygoid fossa. Incomplete stapediaal circulations predominate in populations of *Z. b. brevicauda* and *Z. b. microtinus*; in addition, the bony roof of the mesopterygoid fossa in *Z. b. microtinus* is not perforated by large sphenopalatine vacuities.

KARYOTYPES: Gardner and Patton (1976) reported a diploid number of 84 from Parrita (Costa Rican locality 6), but our specimens from Finca Helechales (Costa Rican locality 3) all have modal counts of 82 chromosomes. Four specimens from Misión Tukuko (Venezuelan locality 79) have 84 chromosomes but one specimen has 82. Chromosome morphology has yet to be described or illustrated for this subspecies.

GEOGRAPHIC VARIATION: Similar to the situation reported above for *Zygodontomys brevicauda brevicauda*, geographic variation

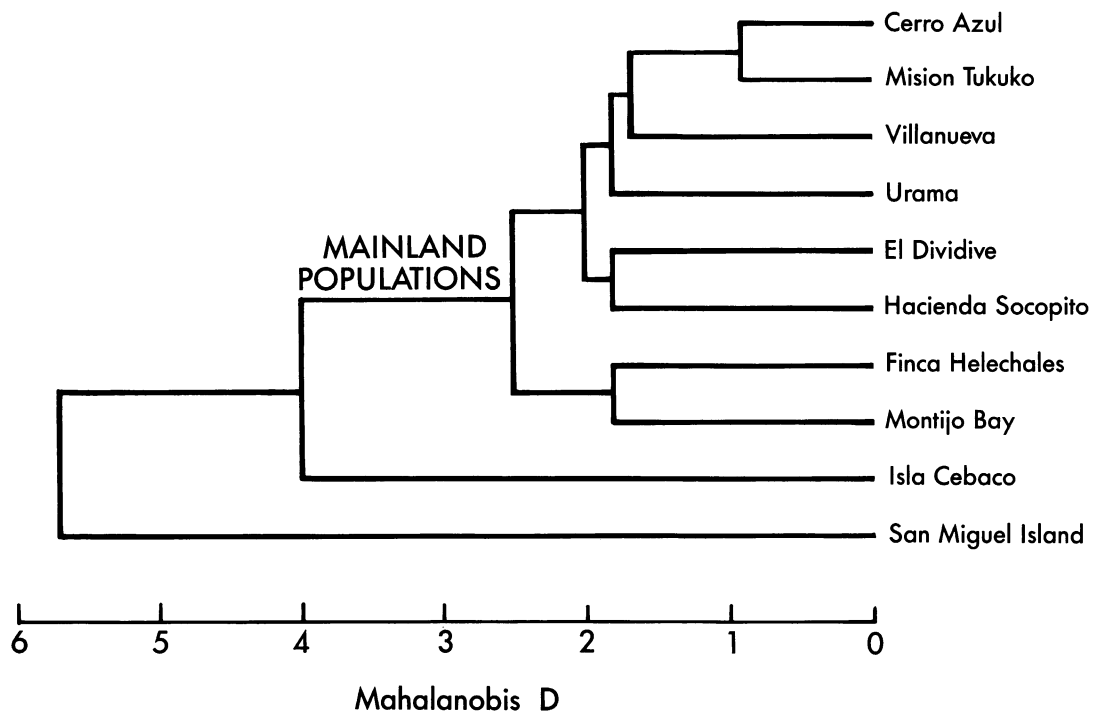


Fig. 29. UPGMA clustering of Mahalanobis distances (D) among 10 population samples of *Zygodontomys brevicauda cherriei*. Sample sizes and geographical information are provided in table 12.

in *Z. b. cherriei* is most evident in comparisons of island and mainland populations. The pelage is more saturated with red and yellow pigments in specimens from the Archipelago de las Perlas (including San Miguel Island and Isla San José) and Isla Cébaco, than in specimens from adjacent mainland localities, which are usually paler and drab grayish

TABLE 18
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys brevicauda cherriei* from Islands on the Continental Shelf of Central America

	Isla Cébaco ^b (24 ♂, 17 ♀, 10 unk.)	San Miguel Island ^c (20 ♂, 17 ♀, 2 unk.)
CIL	28.7 ± 1.71 (25.1–31.8)	30.7 ± 2.01 (26.0–33.4)
LD	8.4 ± 0.64 (6.8–9.6)	9.1 ± 0.80 (7.2–10.3)
LM	4.6 ± 0.11 (4.4–4.8)	4.9 ± 0.19 (4.5–5.3)
BM1	1.3 ± 0.05 (1.2–1.4)	1.5 ± 0.06 (1.4–1.7)
LIF	6.3 ± 0.46 (5.3–7.6)	7.1 ± 0.54 (6.0–8.0)
BR	5.1 ± 0.40 (4.4–5.9)	5.6 ± 0.42 (4.8–6.5)
BPB	2.9 ± 0.28 (2.5–3.7)	3.3 ± 0.37 (2.4–4.0)
BZP	3.1 ± 0.28 (2.4–3.6)	3.5 ± 0.32 (2.8–4.1)
LIB	5.0 ± 0.21 (4.6–5.6)	5.2 ± 0.28 (4.5–5.8)
BB	12.2 ± 0.38 (11.5–13.3)	12.8 ± 0.36 (12.0–13.5)
DI	1.5 ± 0.16 (1.2–1.9)	1.8 ± 0.16 (1.4–2.0)
LOF	10.8 ± 0.64 (9.5–12.0)	11.4 ± 0.70 (9.8–12.6)

^a The mean plus or minus one standard deviation, and the observed range (in parentheses).
^b Panamanian locality 31.
^c Panamanian locality 28.

TABLE 19
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys*
brevicauda cherriei from Mainland Central America

	Finca Helechales ^b (7 ♂, 13 ♀)	Montijo Bay ^c (25 ♂, 8 ♀)	Cerro Azul ^d (23 ♂, 15 ♀)
CIL	26.7 ± 1.70 (23.3–29.2)	25.6 ± 1.58 (23.0–29.2)	26.7 ± 1.68 (22.0–29.4)
LD	7.7 ± 0.63 (6.6–8.6)	7.2 ± 0.63 (6.3–8.6)	7.6 ± 0.65 (6.0–8.9)
LM	4.1 ± 0.10 (4.0–4.4)	4.2 ± 0.12 (4.0–4.5)	4.3 ± 0.16 (4.0–4.6)
BM1	1.3 ± 0.05 (1.2–1.4)	1.2 ± 0.04 (1.2–1.4)	1.3 ± 0.06 (1.2–1.4)
LIF	6.2 ± 0.46 (5.2–6.9)	5.8 ± 0.50 (5.0–7.2)	6.0 ± 0.46 (4.8–6.9)
BR	4.7 ± 0.30 (4.1–5.2)	4.6 ± 0.36 (3.9–5.4)	4.8 ± 0.34 (4.0–5.4)
BPB	3.0 ± 0.26 (2.6–3.4)	2.9 ± 0.28 (2.4–3.4)	3.0 ± 0.31 (2.2–3.6)
BZP	2.9 ± 0.29 (2.4–3.4)	2.7 ± 0.27 (2.2–3.2)	2.9 ± 0.30 (2.1–3.4)
LIB	4.6 ± 0.21 (4.2–5.0)	4.6 ± 0.23 (4.2–5.2)	4.7 ± 0.23 (4.2–5.3)
BB	11.7 ± 0.27 (11.1–12.4)	11.6 ± 0.41 (11.0–12.4)	11.9 ± 0.37 (11.0–12.7)
DI	1.5 ± 0.13 (1.2–1.6)	1.4 ± 0.11 (1.1–1.6)	1.5 ± 0.14 (1.2–1.8)
LOF	10.1 ± 0.71 (8.6–11.4)	9.7 ± 0.58 (8.6–10.8)	10.0 ± 0.52 (8.7–10.8)

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

^b Costa Rican locality 3.

^c Panamanian locality 32.

^d Panamanian locality 26.

brown. Clustering by Mahalanobis D-values (fig. 29) also reveals the phenotypic divergence of island populations: samples from San Miguel Island and Isla Cébaco average larger in all measured dimensions of the skull and dentition (table 18) than samples from adjacent Panamanian mainland localities (table 19).

Mainland population samples of *Z. b. cherriei* exhibit striking uniformity in craniodental measurements from Costa Rica to northwestern Venezuela (compare tables 19 and 20). All mainland samples cluster at D-values of about 2.5 or less (fig. 29) with little evidence of significant hierarchical structure or geographic pattern. Principal components

TABLE 20
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys*
brevicauda cherriei from Northeastern Colombia and Northwestern Venezuela

	Villanueva ^b (16 ♂, 13 ♀)	Misión Tukuko ^c (20 ♂, 16 ♀)	Hacienda Socopito ^d (11 ♂, 11 ♀)	Urama ^e (19 ♂, 11 ♀)
CIL	26.3 ± 1.37 (24.2–28.8)	27.6 ± 2.12 (23.2–31.8)	26.1 ± 1.51 (23.2–29.1)	26.5 ± 1.61 (22.5–29.4)
LD	7.5 ± 0.62 (6.4–8.8)	7.9 ± 0.81 (6.2–9.8)	7.3 ± 0.64 (6.2–9.1)	7.5 ± 0.64 (6.2–8.8)
LM	4.2 ± 0.16 (4.0–4.6)	4.3 ± 0.15 (3.9–4.6)	4.3 ± 0.12 (4.0–4.6)	4.2 ± 0.15 (3.9–4.6)
BM1	1.3 ± 0.05 (1.2–1.4)	1.3 ± 0.06 (1.2–1.4)	1.3 ± 0.05 (1.2–1.4)	1.2 ± 0.05 (1.2–1.4)
LIF	6.0 ± 0.48 (5.1–6.8)	6.1 ± 0.54 (4.8–7.6)	5.8 ± 0.46 (5.0–7.2)	5.7 ± 0.42 (4.9–6.5)
BR	4.7 ± 0.28 (4.1–5.3)	5.0 ± 0.45 (4.1–6.0)	4.6 ± 0.39 (3.8–5.6)	4.8 ± 0.37 (4.2–5.8)
BPB	2.8 ± 0.26 (2.3–3.3)	3.1 ± 0.38 (2.3–3.9)	2.8 ± 0.29 (2.2–3.4)	2.9 ± 0.29 (2.4–3.6)
BZP	2.8 ± 0.28 (2.3–3.4)	3.0 ± 0.32 (2.2–3.8)	2.9 ± 0.33 (2.2–3.6)	2.9 ± 0.30 (2.3–3.6)
LIB	4.6 ± 0.23 (4.1–5.0)	4.8 ± 0.28 (4.2–5.4)	4.5 ± 0.25 (4.2–5.2)	4.7 ± 0.28 (4.0–5.3)
BB	11.6 ± 0.30 (11.0–12.2)	12.1 ± 0.49 (11.0–13.5)	11.7 ± 0.38 (11.1–12.6)	11.7 ± 0.34 (11.2–12.6)
DI	1.5 ± 0.13 (1.2–1.8)	1.6 ± 0.18 (1.2–1.9)	1.5 ± 0.16 (1.2–1.8)	1.5 ± 0.14 (1.2–1.8)
LOF	9.8 ± 0.52 (8.9–10.9)	10.2 ± 0.70 (9.0–11.7)	9.8 ± 0.48 (8.6–10.7)	9.9 ± 0.48 (8.6–10.7)

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

^b Colombian locality 20.

^c Venezuelan locality 79.

^d Venezuelan locality 41.

^e Venezuelan locality 37.

analysis likewise reveals no well-defined pattern of geographic variation among mainland samples of this taxon.

REMARKS: Populations of *Zygodontomys brevicauda cherriei* and *Z. b. brevicauda* are (or were) allopatric in northwestern Venezuela, separated by the Cordillera de Mérida, the Cordillera de la Costa, and forests that formerly occupied the intervening lowlands. At present, there is no evidence of intermediate phenotypes where such might be expected. For example, the large samples of *cherriei* from Ocumare de la Costa (Venezuelan locality 13), Urama (Venezuelan locality 37), and El Tocuyo (Venezuelan locality 49) are close to the presumptive ecogeographic barrier (see fig. 2) but exhibit stapedial frequencies resembling those of Central American populations (table 10). Nevertheless, since the lowlands have been extensively deforested in the Venezuelan states of Aragua, Carabobo, Cojedes, and Yaracuy, genetic contact between these subspecies is inevitable and affords an opportunity to study the consequences of natural hybridization in situ. Alternatively, the two taxa may have diverged sufficiently in allopatry that hybridization is prevented by pre- or postzygotic mechanisms. Either outcome would be of evolutionary interest, but additional morphological, cytological, or molecular characters will be required to serve as sufficient evidence for genetic introgression or isolation. At present, the assignment to subspecies of single specimens or small samples from the region of actual or potential contact is necessarily somewhat arbitrary.

SPECIES EXAMINED: Colombia—*Antioquia*, Caucasia (USNM 4), Cisneros (CMIND 2); *Atlántico*, Ciénaga de Guájaro (USNM 8); *Bolívar*, Boquillas (AMNH 3), Norosí (USNM 4), San Juan Nepomuceno (FMNH 7); *Cesar*, El Orinoco (USNM 13), Río Guaimaral (USNM 15), San Alberto (LACM 13); *Chocó*, Unguía (FMNH 13); *Córdoba*, Montería (FMNH 1, UVM 21), Socorro (FMNH 17); *Cundinamarca*, Caparrapí (ICN 3, USNM 1); *Guajira*, Villanueva (USNM 64); *Huila*, Valle de Suaza (USNM 2), Villavieja (MVZ 9); *Magdalena*, Bonda (AMNH 3, including the type of *sanctaemartae*), Isla de Salamanca (CMIND 3), Mamatoco (AMNH 1), Masinga

Vieja (AMNH 1), Santa Marta (AMNH 1); *Norte de Santander*, El Guayabal (FMNH 2); *Sucre*, Colosó (FMNH 1); *Tolima*, Chicoral (AMNH 1, the type of *fraterculus*), El Triunfo (AMNH 1, the type of *griseus*). Costa Rica—*Puntarenas*, Boruca (AMNH 12, including the type of *cherriei*; FMNH 3), Esterillos Oeste (LACM 2), Finca Helechales (USNM 28), Gromaco (LSU 1), Palmar (AMNH 16), Palmar Sur (LSU 1), Parrita (LACM 1, LSU 4), Río Barú (UMMZ 6), Sardinal (LSU 1). Panama—*Canal Zone*, Barro Colorado Island (USNM 2), Camp Piña (USNM 4), Corozal (USNM 3), Curundu (USNM 1), Empire (USNM 4), Fort Clayton (USNM 12), Fort Kobbe (USNM 6), Fort Sherman (USNM 18), France Field (USNM 3), Frijoles (USNM 4), Gamboa (USNM 3), Gatún (AMNH 5, USNM 4), Madden Road (USNM 10), Red Tank (USNM 1), Rodman Naval Ammo Depot (USNM 37), Summit (USNM 9), Tabernilla (FMNH 2; USNM 11, including the type of *ventriosus*); *Chiriquí*, Armuelles (USNM 8), Boquerón (AMNH 6), El Banco (USNM, skins only), El Valle (USNM 3), Guabalá (USNM, skins only), Progreso (USNM 17), Remedios (TCWC 1), San Juan (USNM 1); *Coclé*, Antón (USNM 3); *Darién*, El Real (AMNH 1, USNM 1); *Los Santos*, Guánico Arriba (USNM, skins only); *Panamá*, Cerro Azul (USNM 63), El Aguacate (USNM 4), Isla San José (USNM 2), San Miguel Island (AMNH 6, FMNH 4, MCZ 26, UMMZ 2, USNM 3); *San Blas*, Armila Village (USNM 26); *Veraguas*, Isla Cébaco (USNM 170), Montijo Bay (UMMZ 51), San Francisco (TCWC 1), Santiago (USNM 5). Venezuela—*Aragua*, Bahía de Cata (MBUCV 1), Ocumare de la Costa (USNM 22); *Carabobo*, Hacienda Saint Jean (MARNR 3, MHNLS 1), Montalbán (USNM 5), Patanemo (MARNR 2, MHNLS 2); *Carabobo* and *Yaracuy*, Urama (USNM 43); *Falcón*, Cerro Socopo (USNM 1); Hacienda Socopito (USNM 33), Mirimire (USNM 1); *Lara*, El Tocuyo (USNM 20), Río Tocuyo (AMNH 10), San Miguel (AMNH 9); *Mérida*, El Vigía (MBUCV 2); *Trujillo*, El Dividive (USNM 99), Santa Apolonia (USNM 8); *Yaracuy*, Finca El Jaguar (MHNLS 1); *Zulia*, El Panorama (FMNH 4), El Rosario (USNM 1), Empalado Savanna (FMNH 2), Hacienda

Rodeo (USNM 2), Misión Tukuko (MHNS and USNM 39), Morotuto (CVULA 1), San Carlos de Zulia (CVULA 6). TOTAL = 1150.

ZYGODONTOMYS BREVICAUDA *MICROTINUS* (Thomas)

Oryzomys microtinus Thomas, 1894: 358.

Zygodontomys microtinus Thomas, 1898: 270.

Zygodontomys brevicauda microtinus Hershkovitz, 1962: 205.

Zygodontomys reigi Tranier, 1976: 1202.

TYPE MATERIAL: The holotype is an old adult (TWC 5) female specimen (BMNH 66.8.11.16) consisting of a fluid-preserved carcass and a cleaned skull with mandibles. The skull is in poor shape: the right zygomatic arch is broken, the pterygoid region and mesopterygoid fossa are damaged, and the coronoid processes of both mandibles are missing; the worn molars retain no details of occlusal morphology. The type was stated by Thomas (1894) to have been collected by "E. Bartlett" in "Surinam," and no other information accompanies the specimen. Husson (1978), however, restricted the type locality to Plantation Clevia, about 8 km NE of Paramaribo (Surinam locality 11), from which many other specimens are now available.

DISTRIBUTION: The coastal savannas of Guyana, Surinam, and French Guiana.

MORPHOLOGICAL CHARACTERS AND COMPARISONS: *Zygodontomys brevicauda microtinus* is distinguished from other subspecies by the predominance of incomplete stapediaal arterial circulations in population samples, and by the absence of well developed sphenopalatine vacuities in the roof of the mesopterygoid fossa. Complete stapediaal circulations predominate in samples of *Z. b. cherriei*, which also possesses large sphenopalatine vacuities. Specimens of *Z. b. brevicauda* usually have incomplete stapediaal circulations, like *Z. b. microtinus*, but differ by exhibiting large sphenopalatine vacuities resembling those of *Z. b. cherriei*.

KARYOTYPES: Tranier (1976) reported a diploid number of 78 from French Guiana but did not describe or illustrate the chromosomes.

GEOGRAPHIC VARIATION: Morphological differences among available samples of *Zygo-*

dontomys brevicauda microtinus are evident in some craniodental measurements (table 21). The large molars of specimens from Cacao are especially notable and probably account for the rather high Mahalanobis D-value (fig. 30) between that sample and the sample from Cayenne which is geographically adjacent (fig. 2, French Guianan localities 2 and 3). Although Cacao and Cayenne cluster together in canonical space, leaving the Paramaribo (Surinam) sample a distant outlier, inspection of measurement means reveals only one univariate difference, in rostral breadth (BR), that might account for this hierarchical structure. I have not been able to discover any qualitative character of the skin, skull, or dentition that differs conspicuously among these samples.

While the morphometric distances represented in figure 30 suggest that significant geographic variation exists within this subspecies, available collections from the Guianas are still too few to permit confident interpretations. In view of the small univariate differences involved, it seems preferable to recognize the obvious similarity of these populations with respect to their common lack of sphenopalatine vacuities rather than emphasize subtle contrasts in measurements that may only represent clinal variation across intervening expanses of unsampled territory.

Tranier (1976) proposed the name *Z. reigi* for populations in French Guiana with diploid counts of 78 chromosomes, contrasting those with populations from Costa Rica, Colombia, and Venezuela with $2N = 84-86$. No karyotypic information is currently available from Surinamese samples, however, and chromosomal data are therefore not germane to the issue of distinguishing *reigi* from *microtinus*. Tranier also cited morphological characters that he believed distinguish populations in French Guiana from those in Surinam:

If the chromosomal distinction between the two *Zygodontomys* [*reigi* and *microtinus*] were not beyond doubt, a morphological difference also distinguishes them. Our adult specimens [from French Guiana] have skulls with maximum length equal to or greater than 30 mm, that is to say, almost always greater than the measured length of *Z. brevicauda microtinus* from Surinam. In addition, the palatine [incisive] foramina of our specimens from French Guiana always extend

TABLE 21
Summary Statistics^a for Craniodental Measurements (in millimeters) of Adult *Zygodontomys
brevicauda microtinus* from Surinam and French Guiana

	Paramaribo ^b (11 ♂, 6 ♀, 10 unk.)	Cayenne ^c (13 ♂, 6 ♀, 2 unk.)	Cacao ^d (12 ♂, 10 ♀, 1 unk.)
CIL	27.5 ± 1.24 (25.6–30.0)	27.0 ± 1.92 (23.8–29.8)	27.1 ± 2.01 (24.1–31.4)
LD	7.9 ± 0.53 (7.3–9.2)	8.0 ± 0.73 (6.8–9.0)	7.8 ± 0.84 (6.6–9.8)
LM	4.2 ± 0.14 (4.0–4.6)	4.3 ± 0.22 (3.8–4.7)	4.7 ± 0.10 (4.5–5.0)
BM1	1.3 ± 0.04 (1.2–1.4)	1.3 ± 0.07 (1.2–1.4)	1.4 ± 0.05 (1.3–1.5)
LIF	6.4 ± 0.43 (5.6–7.2)	6.3 ± 0.49 (5.4–7.2)	6.4 ± 0.53 (5.6–7.5)
BR	4.7 ± 0.23 (4.4–5.2)	5.0 ± 0.40 (4.4–5.7)	5.2 ± 0.40 (4.5–6.0)
BPB	3.0 ± 0.26 (2.5–3.5)	3.0 ± 0.25 (2.6–3.6)	2.9 ± 0.31 (2.4–3.5)
BZP	2.9 ± 0.16 (2.7–3.4)	2.8 ± 0.29 (2.3–3.4)	2.9 ± 0.29 (2.4–3.5)
L1B	4.8 ± 0.21 (4.4–5.3)	4.8 ± 0.26 (4.5–5.4)	4.9 ± 0.17 (4.6–5.4)
BB	12.2 ± 0.24 (11.7–12.8)	12.1 ± 0.47 (11.5–13.2)	12.3 ± 0.30 (11.8–13.2)
DI	1.5 ± 0.09 (1.4–1.8)	1.5 ± 0.17 (1.2–1.8)	1.4 ± 0.13 (1.2–1.6)
LOF	10.1 ± 0.46 (9.4–11.2)	10.1 ± 0.58 (9.0–10.9)	9.9 ± 0.68 (8.8–11.2)

^a The sample mean plus or minus one standard deviation, and the observed range (in parentheses).
^b Surinam locality 11.
^c French Guianan locality 3.
^d French Guianan locality 2.

to about the level of M1 and are more than twice as long as they are wide . . . whereas the examples from Surinam have foramina that never extend to M1 and are almost exactly twice as long as wide . . . (Tranier, 1976: 1202, translated from the French).

No significant differences in cranial length (CIL) are evident among available population samples from French Guiana and Surinam (table 21), nor are differences apparent in absolute or relative dimensions of the incisive foramina. The latter extend to or between the first maxillary molars in most specimens from Surinam and French Guiana alike (table 22).

REMARKS: The availability of the name *reigi* has been questioned by Reig (in Honacki

et al., 1982; and in a footnote to table 16-1 in Reig, 1986). Although Tranier (1976) apparently intended to formally describe the species in a paper cited as “*sous-pressé*” which appears never to have been published, the information provided on page 1202 of his note on karyotypic evolution clearly fulfills the requirements of Articles 11 and 13 of the International Code of Zoological Nomenclature (Code, 1985). *Zygodontomys reigi* is not a nomen nudum and is unambiguously available as a valid species-group name; the holotype (MNHN 1976-361), designated by Tranier (1976), was collected at Cayenne.

SPECIMENS EXAMINED: French Guiana—Bellevue (MNHN 6), Cacao (MNHN 25),

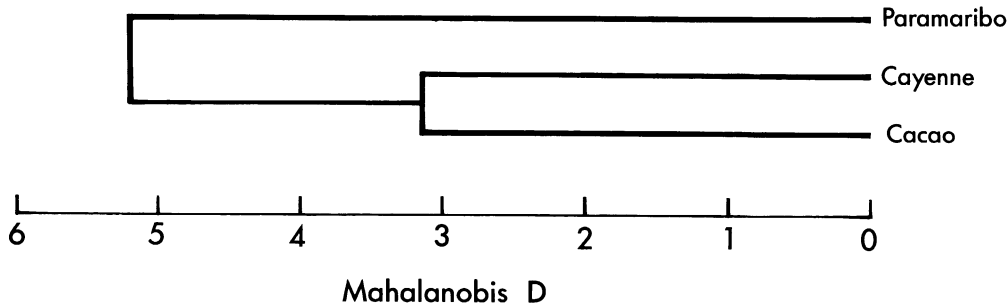


Fig. 30. UPGMA clustering of Mahalanobis distances (D) among three population samples of *Zygodontomys brevicauda microtinus*. See table 12 for sample sizes and geographical information.

Cayenne (BMNH 1; MNHN 23, including the type of *reigi*), Kourou (MNHN 3), Piste de St. Elie (MNHN 2). **Guyana**—*East Demerara–West Coast Berbice*, Great Falls (BMNH 1), Hyde Park (FMNH 1, USNM 1), “R. Demerara” (BMNH 3), Tauraculi (ROM 1), “Uitrlugt Estate” (BMNH 1). **Surinam**—no other locality data (BMNH 1, the type of *microtinus*); *Brokopondo*, Berg en Dal (RMNH 1), Finisanti and Loksihatti (RMNH 3, FMNH 13), Tapoeripa (RMNH 1); *Commewijne*, Gododrai (RMNH 6); *Marowijne*, Albina (AMNH 1), Wiawia Bank (RMNH 3); *Nickerie*, Wageningen (RMNH 7); *Saramacca*, Coppename (RMNH 2), Dirkshoop and La Poule (FMNH 13), Matta (RMNH 1); *Suriname*, Carolina Kreek (FMNH 5), Garnizoenspad (RMNH 2), Kwatta (RMNH 1), Lelydorp and Lelydorpplan (FMNH 1, RMNH 2), Paramaribo (AMNH 1, RMNH 48), Uitkijk (RMNH 1). TOTAL = 181.

UNIDENTIFIED SPECIMENS

Small series of *Zygodontomys brevicauda* from the northern Amazon basin are unassignable to subspecies. Five specimens (AMNH 79401–79404, 80437) from Tabocal (Brazilian locality 1) on the upper Rio Negro all have complete stapedial circulations and large molars (mean LM = 4.6 mm). By contrast, specimens from adjacent populations of *Z. b. brevicauda* (at Belén and Esmeralda, Venezuelan localities 2 and 3; see fig. 2) usually have incomplete stapedial circulations (table 10) and much smaller molars (mean LM = 4.0 mm; table 15). I have been unable to discover any definite information about nonforest habitats on the upper Rio Negro,

TABLE 22
Posterior Extent of the Incisive Foramina in
Samples of *Zygodontomys brevicauda microtinus*

Posterior extent of incisive foramina	Suri- nam ^a	French Guiana ^b
Do not extend to M1 alveoli:	0	0
Extend just to M1 alveoli:	8	2
Extend between M1 alveoli:	28	19
Extend between M1 anterocones:	12	27

^a Vicinity of Paramaribo: samples from Cultuurtuin and Plantation Clevia.

^b Samples from Cacao and Cayenne.

but white sands (which often support savannas or shrublands) are said to be abundant there (Anderson, 1981; Eiten, 1982). The phenotypically distinctive specimens from Tabocal may represent a genetically divergent group of populations associated with distinctive habitats in the Rio Negro basin.

The only specimen (USNM 392078) of *Zygodontomys brevicauda* from Brazilian locality 2 in the Sipaliwini–Rio Paru savannas (see Biogeography and accompanying fig. 38) also has large molars (LM = 4.6 mm) and a complete stapedial circulation. Additional material is clearly desirable, but it is tempting to speculate that related populations may exist in the upper Rio Negro and the Sipaliwini–Rio Paru region, despite the occurrence of typical *Z. b. brevicauda* in the intervening Rio Branco savannas (e.g., the series from Limão and Serra da Lua, Brazilian localities 3 and 4). Collections from the savannas and shrublands of northern Brazil are few, and field expeditions to the area should make special efforts to sample these habitats.

NATURAL HISTORY

The natural history of *Zygodontomys* is as inadequately documented in the literature as are the systematic topics reviewed earlier. Brief accounts of habitats have appeared in various faunal reports, reproduction has been studied in a few wild populations and in several lab colonies, ectoparasites of medical importance have been surveyed in Panama and Venezuela, and a few observations are avail-

able concerning behavior, diets, and predation. There has been no critical evaluation or synthesis of this material, however, and many ecological topics remain uninvestigated. This section summarizes observations recorded in the course of fieldwork from 1984 to 1989 and collates additional information from museum specimens and the literature. These data provide a basis for preliminary infer-

ences about limiting environmental factors and reveal where future ecological research efforts are most likely to be productive.

MAINLAND HABITATS

The following accounts are presented roughly in order of completeness, with those resulting from more extensive fieldwork preceding less detailed descriptions of regions where fieldwork was brief or less ecologically informative.

VENEZUELA, SAN IGNACIO YURUANÍ: The town of San Ignacio is situated near the Río Yuruaní at 850 m elevation in the Gran Sabana, an undulating landscape of forests and savannas drained by the upper Río Caroní (fig. 2, Venezuelan locality 32). Precipitation at San Ignacio averages 2100–2200 mm annually, and the mean annual temperature is about 22–23°C (climatological data courtesy of EDELCA of Venezuela and the Ministerio del Ambiente y de los Recursos Naturales Renovables). Collecting in the vicinity of San Ignacio, from 9–27 June 1986 and 20 June to 7 July 1987, we obtained 231 specimens of nonvolant small mammals from three principal habitat types: evergreen rain forest, savanna, and shrubland.

Evergreen rain forest in the vicinity of San Ignacio (*bosque ombrófilo submesotérmico* of Huber, 1986) occurs over extensive areas of varied topography or as narrow galleries along streams and rivers surrounded by savanna. The forest canopy averages about 30 m in height and the largest trees are often buttressed. Palms are common in the subcanopy and understory and some stilted species are present. Woody lianas are abundantly draped through the canopy, loop from tree to tree in the middle levels of the forest, and form dense tangles with other vines along streams and in clearings made by treefalls. Vascular epiphytes (mostly orchids and bromeliads) are present but not abundant in the canopy. Giant herbs, chiefly aroids and *Heliconia*, together with shrubs and seedling and sapling trees, compose the understory of mature forest growth.

Grassy savanna that is largely devoid of woody plants (*sabana inarbolada mesotérmica* of Huber, 1986) is the other dominant vegetation formation around San Ignacio.

Open hillsides support a sparse growth of grasses (mostly *Trachypogon plumosus*) and sedges, typically about 0.5 m in height, that does not conceal the reddish, mineral soil; conspicuous evidence of erosion is common in such habitats. Shallow swales and some extensive valley bottoms, however, have organic soils and support dense grass- and sedge-dominated meadows; herbaceous vegetation in these communities may reach 1.5 m in height. Marshy areas in the savanna are usually populated by large *moriche* palms (*Mauritia flexuosa*), but this plant community was not sampled by our trapping efforts.

The third distinctive vegetation formation surrounding San Ignacio is a peculiar shrubland known as *arbustal* (fig. 31). Huber (1986, 1989) described this habitat as consisting chiefly of evergreen shrubs (woody plants branched to the ground, that is, without a well-defined trunk) between about 0.5 and 5 m in height; scattered trees of low stature occasionally emerge above the shrub layer, and an inferior stratum of grasses and other herbs is also present. The *arbustales* in which we worked near San Ignacio were all growing on pale, sandy soils eroded from outcrops of soft sandstone; jumbled boulders interspersed with tangled shrubs and stunted trees often composed an almost impenetrable mass of rocks and plants. Most *arbustal* shrubs and trees have hard or leathery leaves, and the sandy soil beneath these thickets is often concealed by a wet but undecayed litter. Areas of sparser shrub cover and small clearings are common, and these support a dense herbaceous growth of grasses, sedges, bracken, terrestrial orchids, and bromeliads. Evidence of past fires was observed in several *arbustales*.

The distribution of collected specimens of small mammals among these habitats exhibits several striking features (table 23). The forest collections were far the most diverse, consisting of three small didelphid marsupials and nine species of rodents. Collections from savanna habitats were the least diverse; only *Akodon urichi*, *Sigmodon alstoni*, and *Cavia aperea* were taken in grassy meadows and other open areas of pure herbaceous cover. The *arbustal* collections were intermediate in species richness, with one marsupial and five rodent species, including all the *Zygodontomys brevicauda* trapped in natural

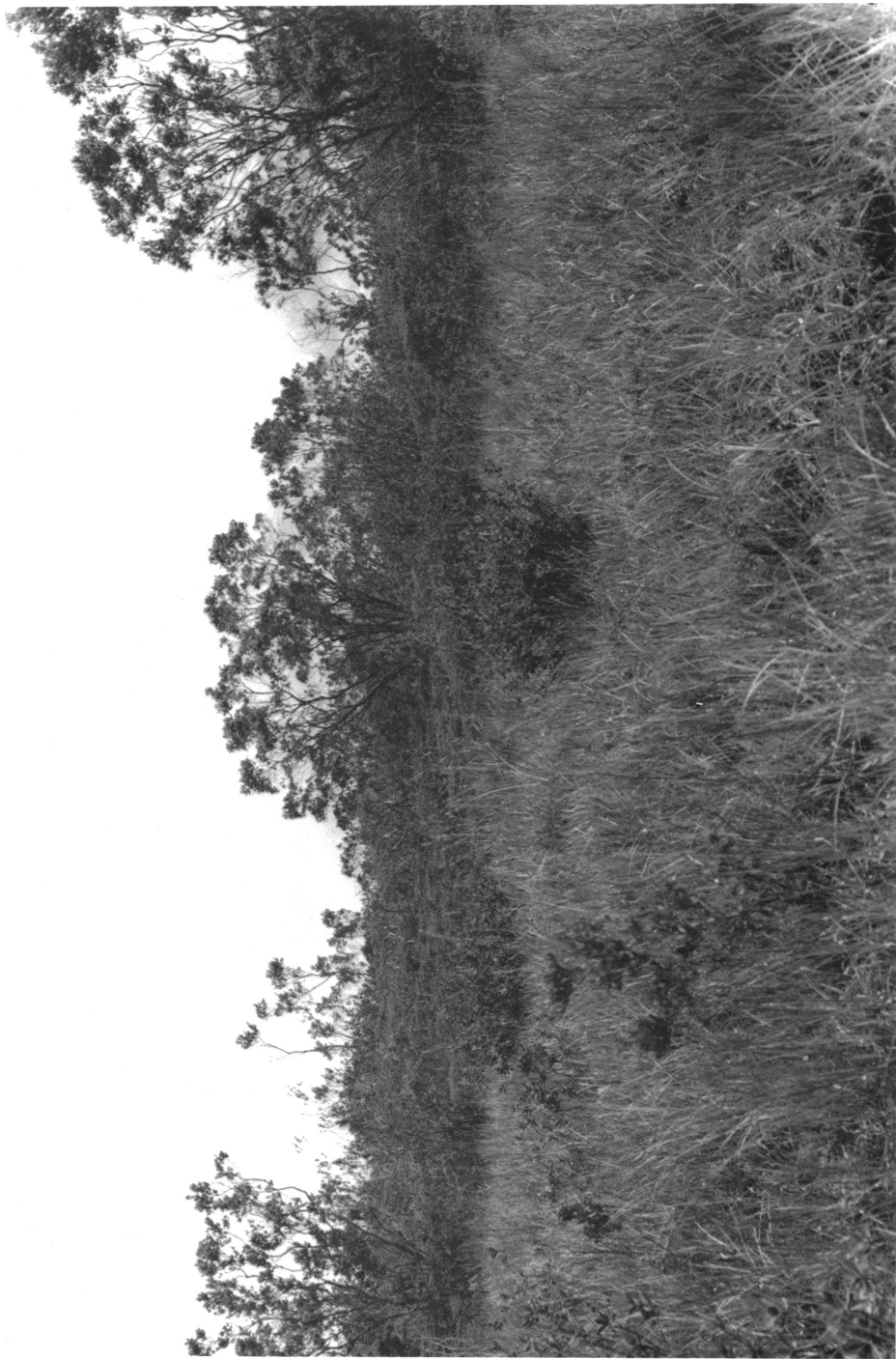


Fig. 31. Grassy clearing in evergreen shrubland (*arbustal*); habitat of *Zygodontomys brevicauda* near San Ignacio Yuruaní, Estado Bolívar, Venezuela. Photographed in July 1987.

TABLE 23
Ecological Distribution of Small Nonvolant Mammals Collected near San Ignacio Yuruaní^a in 1986 and 1987

Species	Habitats ^b			Totals
	Forest	Savanna	Arbustal	
Marsupialia				
Didelphidae				
<i>Marmosa cinerea</i>	1			1
<i>Marmosa murina</i>	8		1	9
<i>Monodelphis brevicaudata</i>	8			8
Rodentia				
Muridae				
<i>Akodon urichi</i>		24	4	28
<i>Neacomys tenuipes</i>	9			9
<i>Nectomys squamipes</i>	2			2
<i>Neusticomys venezuelae</i>	3			3
<i>Oecomys bicolor</i>	5			5
<i>Oecomys trinitatis</i>	9			9
<i>Oligoryzomys fulvescens</i>			5	5
<i>Oryzomys capito</i>	29			29
<i>Oryzomys macconnelli</i>	17			17
<i>Rhipidomys mastacalis</i>	10		32	42
<i>Sigmodon alstoni</i>		4	2	6
<i>Zygodontomys brevicauda</i>			36	36
Echimyidae				
<i>Proechimys guyannensis</i>	19			19
Caviidae				
<i>Cavia aperea</i>		3		3
Totals	120	31	80	231

^a Venezuelan locality 32. Voucher specimens are deposited at AMNH, MHNLS, and USNM.
^b See text for explanation.

habitats (one of our specimens was caught by a boy in the town of San Ignacio). Since we devoted considerable effort, using identical traps and baits, to collecting in forests, savannas, and *arbustales*, it is unlikely that these results are sampling artifacts. Rather, distinctive ecological communities of small mammals appear to be associated with each habitat type. Although a few species were collected in two habitats (e.g., *Rhipidomys mastacalis* in forest and *arbustal*), most seem to be restricted to one. In the context of this report, the absence of *Zygodontomys brevicauda* from rainforest and savanna collections merits emphasis. Forests, savannas, and *arbustales* are juxtaposed in an intricate mosaic throughout the Gran Sabana (Huber,

1986) without extrinsic barriers to prevent dispersal from one to another; since all of these vegetation types were sampled within a few kilometers of San Ignacio, the exclusive occurrence of *Z. brevicauda* in shrublands has no plausible explanation except as reflecting the natural habitat of the species in this region. VENEZUELA, MISIÓN TUKUKO: A small agricultural settlement established by the Capuchin fathers among the Yukpa Indians, Misión Tukuko is located at about 300 m elevation near the base of the Serranía de Perijá west of Lake Maracaibo (fig. 2, Venezuelan locality 79). Annual rainfall averages 2500 mm and annual temperatures average about 26–27°C (Ginés and Foldats, 1953;

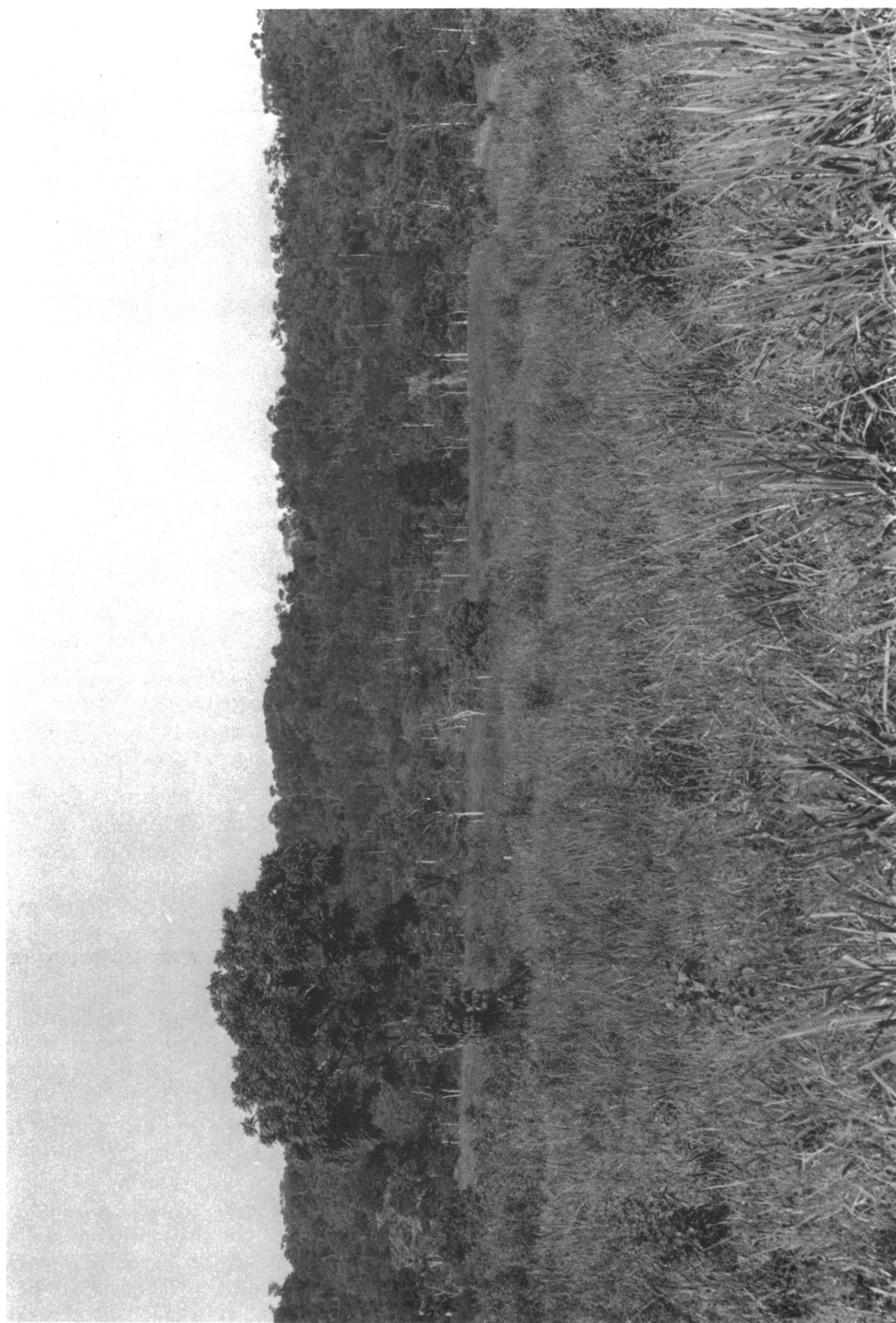


Fig. 32. Deforested landscapes converted to pasture; habitat of *Zygodontomys brevicauda* near Misión Tukuko, Estado Zulia, Venezuela. Photographed in July 1986.

Ruddle and Wilbert, 1983). Collecting in the vicinity of Misión Tukuko from 7–16 July 1986, we obtained 237 specimens of non-volant small mammals from forests and other habitats (table 24).

The entire region surrounding the mission was covered by evergreen rain forest as lately as 40 or 50 years ago, but most level ground has since been cleared for cultivation or animal husbandry. This altered landscape now consists mostly of open meadows and pastures scattered with stumps and rotting logs; only a few isolated trees remain to provide shade (fig. 32). Guava and citrus groves with a dense undergrowth of weeds and bushes, and garden plots in various stages of use or abandonment are other common manmade habitats. Dense thickets of secondary vegetation, consisting mostly of small trees, shrubs, *Heliconia*, large aroids, and cane, occur along small streams and in swampy valley bottoms.

Forests remain on the steep slopes of the adjacent Perijá range, but the natural undergrowth has been cleared and most hillsides are planted with coffee beneath the forest canopy. The canopy trees are very tall, perhaps 40 m on average, and the largest are massively buttressed. Woody lianas and many subcanopy trees also remain. Some of the original undergrowth persists in steep ravines and, even on hillsides planted with coffee, scattered shrubs of other species and a dense ground cover of aroids lends this semicultivated forest a semblance of natural structure. Much of the forest floor consists of knee-high outcrops of eroded limestone, forming an elaborate labyrinth of small caves and narrow crevices.

All of the specimens of *Zygodontomys brevicauda* that we collected near Misión Tukuko were taken in disturbed (secondary) habitats, chiefly moist meadows with scattered stumps and rotting logs, weedy thickets adjacent to streams and swamps, and neglected orchards overgrown with cane and shrubs. We obtained a considerable diversity of other small mammals in such situations, including some (e.g., *Marmosa robinsoni*, *Monodelphis brevicaudata*, and *Heteromys anomalus*) that were also taken in the forest. Since the same traps and baits were used with

TABLE 24
Ecological Distribution of Small Nonvolant Mammals Collected near Misión Tukuko^a in July 1986

Species	Habitats ^b		
	Forest	Other	Totals
Marsupialia			
Didelphidae			
<i>Marmosa robinsoni</i>	1	3	4
<i>Monodelphis brevicaudata</i>	12	3	15
Rodentia			
Heteromyidae			
<i>Heteromys anomalus</i>	24	14	38
Muridae			
<i>Holochilus brasiliensis</i>		1	1
<i>Melanomys caliginosus</i>	3		3
<i>Nectomys squamipes</i>		7	7
<i>Oecomys trinitatis</i>	1	4	5
<i>Oryzomys talamancae</i>	39		39
<i>Rhipidomys venezuelae</i>	4		4
<i>Sigmodontomys alfari</i>		1	1
<i>Zygodontomys brevicauda</i>		50	50
Echimyidae			
<i>Proechimys poliopus</i>	68	2	70
Totals	152	85	237

^a Venezuelan locality 79. Voucher specimens are deposited at MHNLS and USNM.

^b See text for explanation.

roughly equivalent effort to sample forest and nonforest habitats, the absence of *Z. brevicauda* from the forest collections cannot be regarded as a sampling artifact.

VENEZUELA, HATO EL FRÍO: This large cattle ranch is located in the lower Llanos near the Río Apure at an elevation of about 60 m (fig. 2, Venezuelan locality 8). Meteorological data from the lower Llanos are scarce and none appear to be available from the immediate vicinity of Hato El Frío. At San Fernando de Apure, roughly 160 airline km to the east, however, the average annual temperature is 27°C and the average annual precipitation is about 1430 mm (Wernstedt, 1972). Rainfall at Hato El Frío is highly seasonal; virtually all of the annual total falls from April to November; December through March is the dry season when scarcely any precipitation occurs (Ibañez, 1981).

Like most of the lower Llanos, Hato El Frío



Fig. 33. An unflooded grassy *banco* (foreground), inundated savanna, and islands of *mata* vegetation in the lower Llanos; habitat of *Zygodontomys brevicauda* at Hato El Frío, Estado Apure, Venezuela. Photographed in September 1987.

TABLE 25
Ecological Distribution of Small Mammals Collected near Finca Helechales^a in December 1984

Species	Pri- mary for- est	Other habi- tats	To- tals
Marsupialia			
Didelphidae			
<i>Marmosa mexicana</i>	8	5	13
Rodentia			
Heteromyidae			
<i>Heteromys desmarestianus</i>	10		10
Muridae			
<i>Melanomys caliginosus</i>	2	6	6
<i>Nyctomys sumichrasti</i>			2
<i>Oligoryzomys fulvescens</i>	5	9	9
<i>Oryzomys alfaroi</i>	6		5
<i>Peromyscus mexicanus</i>	3		6
<i>Reithrodontomys mexicanus</i>	4		3
<i>Scotinomys teguina</i>			4
<i>Sigmodon hispidus</i>		1	1
<i>Zygodontomys brevicauda</i>		34	34
Echimyidae			
<i>Proechimys semispinosus</i>		1	1
Totals	38	56	94

^a Costa Rican locality 3. Voucher specimens are deposited at USNM.

consists of seasonally inundated savannas (fig. 33) dissected by rivers and streams with wooded banks and scattered with islands of *mata* vegetation (a semideciduous woodland of low stature) growing on slightly elevated soils. During the height of the rainy season most of the savanna is flooded, and only islands of *mata* and elevated grassy areas known as *bancos* provide natural refuges for non-aquatic organisms (Castroviejo and Lopez, 1980).

Collecting at Hato El Frío from 2–8 August 1986 and 3–7 September 1987, we obtained 71 specimens of *Zygodontomys brevicauda* in unflooded grassy savannas, along the shrubby edges of *mata* thickets, in roadside vegetation, in overgrown agricultural fields, on old dikes covered with grasses and shrubs, and in weeds around abandoned ranch buildings. No trapping in the flooded savannas was attempted, nor was substantial effort devoted

to sampling the wooded interiors of *mata* islands or gallery forests. *Sigmodon alstoni* was commonly trapped in most situations where *Z. brevicauda* occurred. Other species of small nonvolant mammals were taken sparingly: *Marmosa robinsoni* and *Oecomys speciosus* in *mata* and gallery forest, and *Oligoryzomys fulvescens* in brushy situations.

COSTA RICA, FINCA HELECHALES: Finca Helechales is a cattle ranch that lies between the Río Guineal and the Río Singri at about 900 m elevation in the foothills of the Cordillera de Talamanca overlooking the Valle de Coto Brus (fig. 1, Costa Rican locality 3). No weather data are available from the immediate vicinity, but the climate of Finca Helechales probably resembles that at San Vito some 30 km to the SE, where the average annual temperature is about 23°C and the annual rainfall is about 4000 mm (Wernstedt, 1972). Collecting between 750 and 1550 m elevation in the vicinity of Finca Helechales from 15 to 25 December 1984, we obtained 94 specimens of small mammals (table 25) in rain forest, scrubby secondary growth, and pastures.

Undisturbed forest habitats in which we collected between 1100 and 1550 m elevation vary physiognomically with exposure to prevailing winds and with local cloud cover. In sheltered valleys between 1100 and 1200 m, the forest is tall and in appearance much like lowland rain forests throughout the humid equatorial Neotropics. At about 1500 m elevation, however, the forests are often shrouded in clouds and have a distinctly montane character; those on windward slopes are stunted, with low, twisted, mossy trees on which epiphytic orchids and bromeliads are common; on leeward slopes the forest is much taller, the trees erect and also mossy, but without many vascular epiphytes except in their upper branches. Sparse undergrowth characterizes primary forest at all elevations.

The 34 specimens of *Zygodontomys brevicauda* collected near Finca Helechales were all taken in moist, grassy pastures with scattered stumps, rotting logs, and low thickets of bracken and blackberry bushes. Despite considerable sampling effort with identical traps and baits in all local habitats, we took no specimens of *Z. brevicauda* in primary forest.

VENEZUELA, FINCA VUELTA LARGA: An old

rice plantation currently used to pasture herds of water buffalo, Finca Vuelta Larga is situated at 10 m elevation near the western limit of the extensive swamps that surround the Orinoco delta (fig. 2, Venezuelan locality 69). Low-lying areas with natural vegetation near the *finca* include seasonally flooded forests, shrubby swamps, and open marshes. All of the high ground has been cleared for human settlements, agriculture, or animal husbandry, and the vegetation is in various stages of disturbance or secondary succession. Collecting in the vicinity of Finca Vuelta Larga from 5 to 17 August 1987, we obtained 179 specimens of small nonvolant mammals, including 37 *Zygodontomys brevicauda*.

All of our collecting at Finca Vuelta Larga was in disturbed or successional habitats: in wet grass along the edges of marshy pastures, in shrubby thickets surrounded by pastures on high ground, in old garden plots and orchards overgrown with weeds and vines, and in a 14-year-old patch of secondary forest. *Zygodontomys brevicauda* was collected in all of these situations, but with different associations of sympatric species. *Marmosa cinerea*, *M. murina*, *Monodelphis brevicaudata*, *Heteromys anomalus*, *Oryzomys capito*, and *Proechimys trinitatis* were found to be largely or exclusively restricted to secondary forest habitats. *Oligoryzomys fulvescens* was most abundant in shrubby pastures but was also taken commonly along the edge of secondary forest. *Sigmodon alstoni* and *Oecomys trinitatis* were taken in overgrown garden plots, while *Holochilus brasiliensis* was only trapped along the wet edges of marshy pastures. *Akodon urichi* was common in all sampled habitats.

ISLAND HABITATS

TRINIDAD AND TOBAGO, TOBAGO: Situated on the continental shelf of South America northeast of Trinidad, the island of Tobago is 42 km long, and 12 km across at its widest point; the topography is mountainous with a maximum elevation of 580 m. Annual rainfall varies from about 1400 mm in the southwest to almost 2400 mm in the northeast, and the average annual temperature is probably about 26°C (Beard, 1944). In the course of fieldwork from 17 to 24 January 1989, we

collected 122 specimens of small mammals in the vicinity of Charlotteville and Pigeon Peak, near the northeastern tip of the island (table 26). Natural habitats on Tobago were described by Beard (1944) whose more detailed accounts are consistent with our own field observations summarized below.

We trapped in lowland rain forest (fig. 34) at about 200–300 m elevation. The canopy is very high, perhaps 35 to 40 m, and many of the largest trees develop huge buttresses; tall, graceful palms (*Euterpe* sp.) are common in the subcanopy. Woody lianas are present but not very abundant. Vascular epiphytes, mostly orchids and bromeliads, are occasionally visible in the canopy but not at lower levels in the forest where tree trunks are generally smooth and without clinging vegetation. The understory is open and consists mostly of sapling trees, seedling palms, shrubs (*Piper* sp., Rubiaceae, and Melastomaceae are common), and a few giant herbs (mostly gingers and aroids). A sparse leaf litter barely conceals the underlying clayey soil.

We also trapped in montane rain forest (fig. 35) at about 520 m elevation on the Main Ridge, which was often enveloped by clouds and soaked by misting rain. This very wet forest is not as tall as the lowland forest, with a canopy only about 25 m in height; the trees forming the canopy are of lesser girth than those of lowland forest and are seldom buttressed (the buttresses, when present, are small and do not resemble the planklike structures of lowland trees). Unlike the smooth, naked boles of trees in lowland forest, tree trunks in the montane forest are densely invested with climbing ferns, aroids, orchids, and bromeliads from the upper branches to ground level. Many trunks are mossy but the moss layer is thin and does not form thick mats. Tangled vines, including woody species, are everywhere. The undergrowth includes seedling palms, sapling trees, shrubs, tree ferns, Cyclanthaceae, gingers, and *Heliconia*. A shallow humus is present beneath a superficial litter of leaves and twigs.

Zygodontomys brevicauda was collected in undisturbed lowland and montane rain-forest habitats as well as in slash-and-burn garden plots, secondary roadside vegetation, and cacao groves in various stages of active cultivation or neglect. The other small mammal species that we collected at this locality

TABLE 26
Ecological Distribution of Small Nonvolant Mammals Collected near Charlotteville,^a Tobago, in January 1989

Species	Primary forest		Other habitats ^b	Totals
	Lowland	Montane		
Marsupialia				
Didelphidae				
<i>Marmosa robinsoni</i>	2	2	1	5
<i>Marmosa murina</i>	2	4	6	12
Rodentia				
Heteromyidae				
<i>Heteromys anomalus</i>	4	10		14
Muridae				
<i>Akodon urichi</i>	6	1	27	34
<i>Oecomys trinitatis</i>			3	3
<i>Zygodontomys brevicauda</i>	5	7	42	54
Totals	19	24	79	122

^a Trinidad and Tobago locality 1. Voucher specimens are deposited at AMNH.

^b See text for explanation.

also occur both in rain forests and in disturbed or successional plant communities.

SUMMARY OF HABITAT INFORMATION

Published and unpublished sources document the occurrence of mainland populations of *Zygodontomys* in a wide variety of lowland habitats, with the important and conspicuous exception of mature, closed-canopy rain forests. Most available habitat descriptions concern populations of *Z. brevicauda*, but fieldnotes and labels accompanying specimens of *Z. brunneus* record collections made in similar ecological circumstances. Interspecific habitat divergence is to be expected, if at all, where *Z. brevicauda* and *Z. brunneus* occur sympatrically in the upper Magdalena valley of Colombia, and should be the object of careful field investigations in that region.

Altitudinal data are available from 186 localities whose frequency distribution (fig. 36) reveals that *Zygodontomys* is most often collected below 100 m elevation. Nevertheless, collections from elevations exceeding 500 m are not uncommon and there are three well-documented records between 1200 and 1300

m.⁷ Within the latitudinal limits occupied by the genus (about 0 to 12°N), elevation largely determines the average annual temperatures encountered: from about 26–28°C near sea level to 20–22°C at 1200 m. Monthly temperatures can be expected to fluctuate only slightly about these annual averages since the mean difference between the coldest and warmest months at tropical localities seldom exceeds 4–5°C.

The annual rainfall in regions inhabited by *Zygodontomys* varies from several meters (e.g., 3900 mm at Palmar Sur, Provincia Puntarenas, Costa Rica) to less than a meter (e.g., 400 mm at Cumaná, Estado Sucre, Venezuela; both data from Wernstedt, 1972), but

⁷ One locality in excess of 1300 m elevation is not represented in the frequency histogram (fig. 36). The collection in question consists of a single specimen (AMNH 176323) represented by a skin and skull; according to the skin label, which appears not to have been prepared in the field, the animal was collected by E. McGuire on 12 February 1953 on Churi-tepui (fig. 2, Venezuelan locality 22) at an elevation of 6400 ft (1969 m). Since the elevation is so much greater than any other at which the genus has been collected, and because no corroborating fieldnotes or other original documents can be found, this datum should not be accepted uncritically.



Fig. 34. Lowland forest at about 200 m elevation; habitat of *Zygodontomys brevicauda* near Charlotteville, Tobago. Photographed in January 1989.



Fig. 35. Montane forest at about 520 m elevation; habitat of *Zygodontomys brevicauda* near Charlotteville, Tobago. Photographed in January 1989.

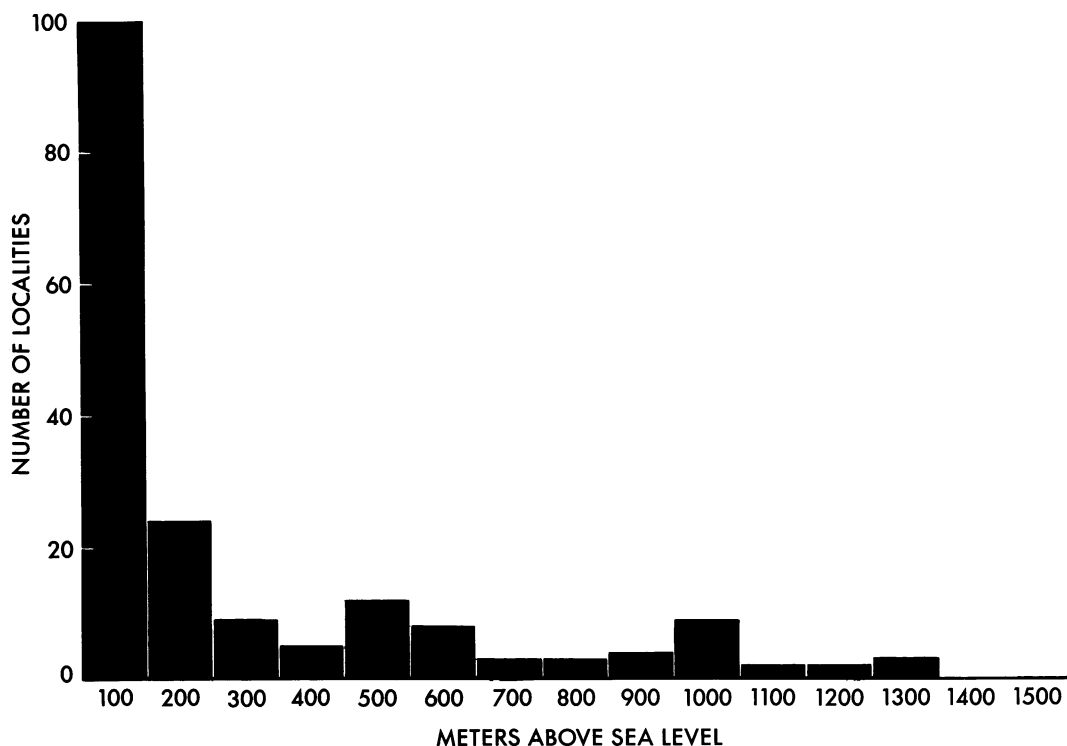


Fig. 36. Frequency histogram of elevations of 186 collection localities of *Zygodontomys* species.

typical values cluster between 1000 and 2000 mm. At some localities, substantial precipitation occurs throughout the year; the majority, however, experience pronounced dry seasons of several months duration when little or no precipitation occurs (fig. 37).

Within these broad abiotic environmental tolerances, mainland populations of *Zygodontomys* occupy a variety of nonforest plant communities. Natural macrohabitats include thornscrub and savannas along the Pacific littoral of Panama, seasonally inundated grasslands and deciduous savanna woodlands in the Llanos, the Caribbean coastal deserts of Colombia and Venezuela, and the evergreen shrublands (*arbustales*) of the Gran Sabana. *Zygodontomys* is also abundant in anthropogenic habitats such as pastures and open rangelands denuded of natural forest cover, abandoned garden plots, the overgrown margins of cultivated fields, orchards with dense herbaceous undergrowth, and in weedy plots within human settlements. In some regions, *Z. brevicauda* is an agricultural pest (Woronecki, 1973; Husson, 1978), and,

throughout most of its geographic range, this is probably the commonest indigenous mammal in close contact with man.

Microhabitats favored by continental populations of *Zygodontomys* always include an herbaceous ground cover that is usually interspersed with woody plants growing in small thickets; stumps, logs, rocks, boards, trash, and other sheltering objects are also characteristic of sites where these rodents are abundant. Extensive areas of harsh, dry grasses and sedges growing in sparse clumps on bare, mineral soils do not appear to provide optimal habitats. Instead, a dense growth of grasses and herbaceous dicots with leaves that crush easily between the fingers is the best predictor of trap success, especially in moist situations adjacent to streambanks, brushy thickets, stumps, logs, and rocks. In desert regions, *Zygodontomys* is probably restricted to the vicinity of water sources.

The absence of *Zygodontomys* from undisturbed rain forests on the Central and South American mainland is abundantly documented. Our collections at San Ignacio

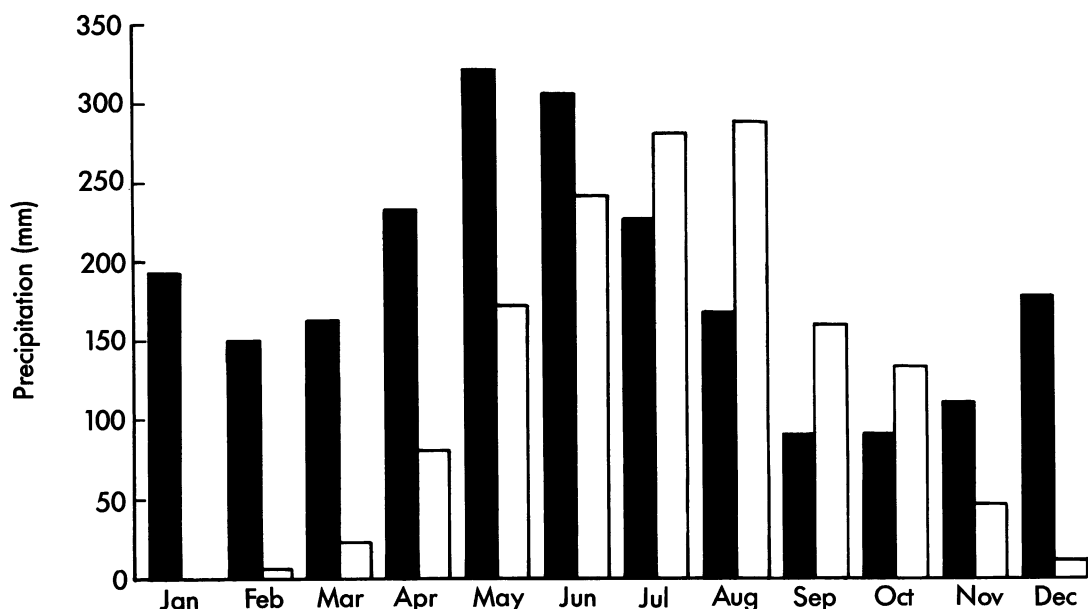


Fig. 37. Monthly rainfall at Paramaribo (solid bars) and at San Fernando de Apure (open bars), illustrating differences in seasonality for two regions where *Zygodontomys brevicauda* is abundant. Paramaribo (Surinam locality 11, fig. 2) receives an average of 2210 mm annually with substantial precipitation in every month of the year; the average difference between the driest and wettest months at this locality is roughly fourfold. San Fernando de Apure (near Venezuelan locality 8, fig. 2) receives an annual average of 1431 mm, but little rain falls during a pronounced dry season; the average difference between the driest and wettest months is almost 300-fold. Data from Wernstedt (1972), based on 30 years of weather records at Paramaribo and 31 years at San Fernando de Apure.

Yuruaní, Misión Tukuko, and Finca Helechaes simultaneously sampled rain forests and adjacent nonforest habitats with identical traps and baits. Taxonomically diverse rainforest communities of small mammals were discovered at each locality, but not a single specimen of *Z. brevicauda* was taken in forests despite the abundance of this species in open vegetation that was sometimes only a few hundred meters away. Summarizing habitat data from 833 specimens collected throughout Venezuela, Handley (1976) also found *Z. brevicauda* to be absent from rainforest interiors, but recorded its occurrence in grassy openings and along forest margins. Goldman (1920), Aldrich and Bole (1937), Tate (1939), Hershkovitz (1962, and in litt.), Handley (1966), Fleming (1970), and Husson (1978) provided similar observations from Panama, Colombia, Venezuela, Brazil, and Surinam.

The distinction between rain forest and other arborescent plant communities in which

Zygodontomys can sometimes be found is important. Mature rain forests are taxonomically diverse plant communities dominated by evergreen trees that, in the lowlands, form a closed canopy 30 m or more in height (Richards, 1952). Lowland rainforest trees typically have straight, smooth trunks that are unbranched except near the canopy; large trees frequently develop huge plank buttresses. Other characteristic plant growth-forms in lowland rain forests are thick-stemmed lianas (woody climbers) and giant herbs (in the families Araceae, Cyclanthaceae, Marantaceae, Musaceae, and Zingiberaceae). The undergrowth of mature lowland rain forest is not very dense and graminoids (sedges and grasses) are absent or uncommon.

By contrast, the savanna woodlands in which August (1981, 1984), O'Connell (1981, 1989), and Vivas (1984) studied populations of *Zygodontomys brevicauda* in the Llanos are composed of a few species of palms and deciduous trees that form an irregular canopy

only 8–12 m in height; grasses and sedges are abundant in the undergrowth and the overall aspect of these thickets is quite unlike that of rain forest (photographs in Troth, 1979). Fleming (1970) reported *Z. brevicauda* from “Dry Tropical Forest” at Rodman Naval Ammo Depot (Panamanian locality 12), but the canopy of this semideciduous growth was discontinuous and only 4 to 20 m in height (Fleming, 1971); the study area was also penetrated by paved roads with grassy margins that “. . . were undoubtedly responsible for the occurrence of otherwise typical inhabitants of grasslands (for example, *Sigmodon hispidus* and *Zygodontomys [brevicauda]*) inside the forest” (Fleming, 1970: 474). Mainland populations of *Zygodontomys* sometimes occur in arborescent secondary growth that replaces rainforest vegetation destroyed by slash-and-burn agriculture or wholesale logging operations; such seral plant communities often have a dense herbaceous undergrowth, however, and are easily distinguished from mature forest.

In striking contrast to the ecological distribution of *Zygodontomys* on the Central and South American mainland is the presence of *Z. brevicauda* in undisturbed lowland and montane forests on the island of Tobago. Physiognomically, these insular habitats appear similar to rain forests on the adjacent South American mainland, but Tobagoan forests are depauperate in species of small mammals: in addition to those listed in table 26, only *Echimyus armatus* and *Rhipidomys mastacalis* (or *nitela*) are known from the Recent fauna (Goodwin, 1961, 1962), whereas mainland rain forests always support more diverse communities (e.g., table 23 of this report and table 43 of Voss, 1988). Published information from Trinidad and the Pearl Archipelago of Panama suggests that Tobago is not the only continental-shelf island on which *Zygodontomys* occurs in forests.

1. From September 1959 to December 1964 the Trinidad Regional Virus Laboratory carried out an extensive survey of arboviruses and their vertebrate host populations in a tract of lowland evergreen rain forest on Bush Bush “Island,” actually a peninsula of elevated land surrounded on three sides by the Nariva Swamp in eastern Trinidad (Downs et al., 1968). The faunal inventory

TABLE 27
Numbers of Small Nonvolant Mammals (excluding introduced species) Trapped in Bush Bush Forest, Trinidad, by the Trinidad Regional Virus Laboratory from August 1960 to October 1963^a

Species	Specimens
Marsupialia	
Didelphidae	
<i>Marmosa robinsoni</i> ^b	13
<i>Marmosa</i> sp.	15
Rodentia	
Heteromyidae	
<i>Heteromys anomalus</i>	423
Muridae	
<i>Nectomys squamipes</i>	37
<i>Oecomys trinitatis</i> ^c	46
<i>Oligoryzomys fulvescens</i> ^d	1
<i>Oryzomys capitor</i> ^e	696
<i>Zygodontomys brevicauda</i>	479
Echimyidae	
<i>Proechimys trinitatus</i> ^f	19
Total	1729

^a From table 2 of Worth et al. (1968). Bush Bush Forest is Trinidad and Tobago locality 6. Voucher specimens are deposited at AMNH.

^b Reported as *Marmosa mitis*.

^c Reported as *Oryzomys concolor*.

^d Reported as *Oryzomys delicatus*.

^e Reported as *Oryzomys laticeps*.

^f Reported as *Proechimys guyannensis*.

was not complete, but the numerical results (table 27) clearly document the abundance of *Zygodontomys brevicauda* in sympatry with some of the small didelphid marsupials and rodent species that are characteristic of lowland rain forests on the Venezuelan mainland.

2. The collector W. W. Brown, Jr., trapped 68 specimens of *Zygodontomys brevicauda* between 20 April and 8 May 1900 on San Miguel Island (Isla del Rey) in the Gulf of Panama. According to Bangs (1901: 631–644) who described Brown’s material, “It [San Miguel Island] is composed of low-lying hills clothed in heavy tropical forest, hot, damp, and unhealthy . . . *Z. soersus* [= *Z. brevicauda*] was an abundant animal on San Miguel Island, inhabiting the dense, swampy woods, and Mr. Brown found no difficulty in trap-

ping it in numbers." *Marmosa robinsoni*, *Proechimys semispinosus*, and *Diplomys labilis* are the only other species of small non-volant mammals known from San Miguel Island (Handley, 1966).

Few as they are, these additional observations of insular habitats indicate that consistent ecological differences may exist between island and mainland populations of *Zygodontomys brevicauda*. The possible historical origins of such differences are discussed in the concluding section of this monograph.

OTHER TOPICS

CIRCADIAN ACTIVITY: Most of the 282 specimens of *Zygodontomys brevicauda* that my colleagues and I collected in the field were trapped between dusk and dawn. Although baited traps remained open during daylight hours, traps found empty in the early morning seldom contained *Zygodontomys* when the lines were revisited in the late afternoon. By contrast, specimens of *Akodon urichi* were often caught during the day in the same trap-lines that took *Z. brevicauda* at night, both on the Venezuelan mainland (at Finca Vuelta Larga and San Ignacio Yuruani) and on Tobago. Enders (1935), Aldrich and Bole (1937), and O'Connell (1981) also reported nocturnal habits for *Z. brevicauda*. The trapping results of Ibañez (1980) and Vivas et al. (1986) documented peak activity between about 1800 and 2000 hours in the Venezuelan Llanos.

SPATIAL USE OF HABITATS: All but one of the 282 specimens of *Zygodontomys brevicauda* that we collected at the localities described above were trapped on the ground despite the fact that many traps were set in trees. Even on Tobago, where *Z. brevicauda* occurs in rain forest, and where special efforts were made to sample arboreal microhabitats, only one of the 54 specimens collected was taken off the ground (the single animal in question was trapped about 30 cm above the forest floor in the broad, leaf-filled crotch of a spreading tree). Handley (1976) reported that all of the 833 specimens of *Z. brevicauda* collected by the Smithsonian Venezuelan Project were taken on the ground. August (1981, 1984) contrasted *Z. brevicauda*, which he took only in Sherman traps set on the

ground, with other species of small mammals from the same habitats that were commonly taken in Sherman traps set in trees. Presumably, *Zygodontomys* is almost exclusively terrestrial in the course of its nocturnal activities. Nests, described by Enders (1935), Aldrich and Bole (1937), and O'Connell (1981), are made of grass in shallow burrows, in cracks in the ground (caused by drought in seasonally flooded areas), under tree roots, or directly on the soil surface.

DIET: Captive colonies of *Zygodontomys brevicauda* thrive on commercial laboratory rodent diets, although higher-protein supplements and fresh vegetables are avidly consumed when they are provided (Voss et al., in press). O'Connell (1981) offered wild-caught animals a variety of foods from natural habitats in the Llanos and found that *Z. brevicauda* consumed fruit, seeds, grass (but sparingly), fungi, and adult and larval insects. Fleming (1970: 483) examined the stomach contents of 20 specimens of *Z. brevicauda* collected during the rainy season in Panama:

Sixteen of the stomachs contained mostly fruit pulp and seeds but little green plant material. Two stomachs were full of insect parts . . . and two others contained an estimated 50 percent insect parts by volume. Chitinous insect remains were found in most stomachs containing predominantly plant material.

Fleming (1970: 485) contrasted this diet with that of sympatric *Sigmodon hispidus* and observed that the latter "... appeared to be feeding on more plant material, especially leaves and stems, and fewer insects . . ." than *Z. brevicauda*.

REPRODUCTION: The reproduction and development of captive *Zygodontomys brevicauda* from the Llanos were described by Aguilera (1985) and Voss et al. (in press). *Z. brevicauda* is a spontaneous ovulator that gives birth to litters of 1 to 11 young (4 and 5 are modal values) after a gestation of 25 days. There is a postpartum estrus and implantation is not delayed by lactation. The neonates, which typically weigh 3 or 4 g each, are sparsely haired and appear naked; the eyes are closed at birth and the dentition is unerupted, but the pinnae are unfolded and the digits are all separated. The juvenile pelage is well grown by the fifth day postpartum, and eyes open on day 6. Lower incisors begin to erupt on day 4 and upper incisors on day

TABLE 28
Numbers of Embryos in Wild-Caught Female *Zygodontomys brevicauda*

Locality ^a	Sample size ^b	Number of embryos		Source
		Mean	Observed range	
Costa Rica				
3. Finca Helechales	4	4.0	3–5	this study
Panama				
Canal Zone ^c	7	3.7	3–5	Fleming, 1970
32. Montijo Bay	"many"	—	2–11	Aldrich and Bole, 1937
Venezuela				
8. Hato El Frío	29	4.4	1–7	Ibañez and Moreno, 1982
8. Hato El Frío	9	5.8	4–8	this study
69. Finca Vuelta Larga	5	4.0	2–6	this study
79. Misión Tukuko	9	4.9	4–7	this study

^a Numbered localities are mapped in figs. 1 and 2.

^b Number of females in which embryos were found.

^c Specimens were collected either at Fort Sherman (Panamanian locality 6) or Rodman Naval Ammo Depot (Panamanian locality 12).

6; the first upper and lower molars initiate eruption simultaneously on day 8 when the first traces of solid food appear in stomachs. By day 16 the young subsist entirely on solid food. Females reach sexual maturity at about three to four weeks of age, males at six to eight weeks. Bates and Weir (1944) and Worth (1967) provided reproductive observations from captive colonies of *Z. brevicauda* in Colombia and Trinidad, respectively.

Embryo counts from wild-caught female *Zygodontomys brevicauda* are summarized in table 28.

The results from several field studies of *Zygodontomys brevicauda* suggest that reproduction is continuous even in conspicuously seasonal habitats. August (1981, 1984), O'Connell (1981, 1989) and Vivas (1984) observed immature animals and lactating or pregnant females throughout the year in the Llanos where annual cycles of flooding and drought dramatically transform the physical and biological landscape. Fleming (1970) also suggested that *Z. brevicauda* reproduces aseasonally, citing pregnancies that he and Enders (1935) recorded in both rainy and dry seasons in Panama. Most large museum series of *Zygodontomys* contain juveniles, adults, and old adults regardless of the season in which collections were made. While it seems reasonable to conclude from these observations that reproduction in *Z. brevicauda* probably is

aseasonal, it should be noted that the field studies by August, O'Connell, and Vivas employed only mark-and-recapture methods and that no autopsies were performed to confirm judgments of reproductive condition based on external criteria.⁸

RELATIVE AND ABSOLUTE ABUNDANCE: The data provided in tables 23–26 suggest that *Zygodontomys brevicauda* is not rare in the habitats where it occurs, but we devoted special attention to collecting this species and the numbers obtained therefore cannot be accepted as unbiased estimates of relative abundance. The results of general faunal survey efforts in Panama (Handley, 1966), Venezuela (Tate, 1939; Handley, 1976), Trinidad (Worth et al., 1968; see table 27 of this report), and Surinam (Husson, 1978), however, presumably lack conscious bias and suggest that *Z. brevicauda* is among the most abundant (or at least one of the most trappable) species of small mammals throughout its ecogeographic range.

Mark-and-recapture studies have provided

⁸ Vaginal patency, one external criterion of female reproductive activity recorded by August, O'Connell, and Vivas, is wholly unreliable. Vaginal closure membranes disappear and reappear spontaneously in unmated captive females (Voss et al., in press); furthermore, I have autopsied several wild-caught females with "imperfect" vaginae and embryos in utero.

estimates of absolute abundance of *Zygodontomys brevicauda* in seasonally inundated habitats of the Venezuelan Llanos. O'Connell (1981, 1989) found maximum densities of about 40 animals/hectare in one dry season, followed by a precipitous decline as her trapping area was flooded in the following wet season. Vivas (1984) reported densities of over 100 animals/hectare in the late dry season and early wet season for two consecutive years and (like O'Connell) observed dramatic declines in numbers as the wet season progressed and his trapping grid was inundated. The much higher maximum densities reported by Vivas could reflect a real temporal or habitat difference between his study and O'Connell's, but might also be attributed to differences in sampling design. Vivas deployed his traps in a square grid at 10 m intervals; O'Connell's traps, placed at 20 m intervals, might have failed to capture many individuals resident on her grid if home ranges of *Z. brevicauda* are small. Neither Vivas nor O'Connell could distinguish between emigration and in situ mortality as the cause of the population declines they observed, but many animals probably migrate to unflooded habitats as water levels rise in the rainy season (Soriano, 1977; cited by O'Connell, 1989). August (1981, 1984) also carried out mark-and-recapture studies of small mammals in the Llanos, but his data on *Z. brevicauda* are too sparse for credible estimates of population densities.

PREDATORS: Haverschmidt (1968) identified *Zygodontomys brevicauda* as one of the main prey of barn owls (*Tyto alba*) in Surinam, and also recorded it in the diets of striped owls (*Asio clamator*) and white-tailed kites (*Elanus leucurus*); Husson (1978) confirmed Haverschmidt's observations and also reported *Z. brevicauda* in the diet of gray hawks (*Buteo nitidus*). Small mammals constituted 26 percent by volume of the contents of 104 stomachs of the fox *Cerdocyon thous* examined by Bisbal and Ojasti (1980) in Venezuela, and *Z. brevicauda* was the commonest identifiable species in that fraction. *Z. brevicauda* is also known to be eaten by *Felis jagouaroundi* (Bisbal, 1986). In view of their numerical abundance and wide ecogeographic distribution, species of *Zygodontomys* are

probably common in the diets of many carnivorous vertebrates.

ECTOPARASITES: Information concerning the ectoparasites of *Zygodontomys* is available from faunal surveys of medically important arthropod taxa in Panama and Venezuela: laelapid and macronyssid mites, ticks, chiggers, lice, and fleas. A total of 55 species in these groups are known to infest *Z. brevicauda* (table 29). More ectoparasites are known from *Z. brevicauda* in Venezuela (48 species) than in Panama (24 species), but this difference probably reflects the very large numbers of *Z. brevicauda* collected by the Smithsonian Venezuelan Project (833 according to Handley, 1976). Many parasite records for *Z. brevicauda* in both Panama and Venezuela are based on just one or a few specimens and may represent contaminations (accidental transfers from another host species made in the course of field collecting) or infrequent natural infestations that do not reflect normal host-parasite relationships.⁹ Ectoparasites that commonly infest *Z. brevicauda* in both Panama and Venezuela include the laelapid mite *Laelaps dearmasi*, unidentifiable immature ticks of the ixodid genus *Amblyomma*, a diversity of chiggers (Acari, Trombiculidae), the louse *Hoplopleura nersoryzomydis*, and fleas of the rhopalopsyllid genus *Polygenis*. The laelapid mite *Androlaelaps fahrenheitzi* and the macronyssid mite *Ornithonyssus bacoti* commonly infest *Z. brevicauda* in Venezuela, but appear less commonly on *Z. brevicauda* in Panama.

In Panama and Venezuela, *Zygodontomys brevicauda* is the principal host of the mite *Laelaps dearmasi*, the louse *Hoplopleura nersoryzomydis*, and the only known host of the chigger *Atelepalme smarma*, but its remaining ectoparasites commonly occur on other vertebrate species as well. Ticks, most chiggers, and some fleas (pulicids and *Rhopalopsylla* species) known to infest *Z. brevicauda*

⁹ Sucking lice of the genus *Fahrenheitzia*, for example, normally parasitize heteromyid rodents; the occasional infestation of *Zygodontomys brevicauda* by *F. hertigi* in Panama and by *F. schwartzi* in Venezuela presumably represent natural transfers from sympatric *Heteromys desmarestianus* and *H. anomalus*, respectively (Wenzel and Johnson, 1966; Johnson, 1972).

TABLE 29
Arthropod Parasites of *Zygodontomys*
brevicauda In Panama and Venezuela

Taxa	Occurrence ^a	
	Pan- ama	Vene- zuela
ARACHNIDA (Acari)		
Mesostigmata		
Laelapidae ^b		
<i>Gigantolaelaps canestrinii</i>		+
<i>Gigantolaelaps gilmorei</i>	+	
<i>Gigantolaelaps goyanaensis</i>	+	+
<i>Gigantolaelaps oudemansi</i>	+	
<i>Gigantolaelaps wolffsohni</i>	+	
<i>Laelaps dearmasi</i>	++	++
<i>Laelaps ovata</i>		+
<i>Laelaps pilifer</i>		+
<i>Tur amazonicus</i>		+
<i>Tur apicalis</i>		+
<i>Tur subapicalis</i>		+
<i>Mysolaelaps parvispinosus</i>		+
<i>Septolaelaps heteromys</i>		+
<i>Androlaelaps fahrenheiti</i>	+	++
<i>Androlaelaps hirsuta</i>		+
<i>Androlaelaps projecta</i>		+
<i>Androlaelaps rotundus</i>		+
Macronyssidae ^d		
<i>Ornithonyssus bacoti</i>	+	++
<i>Acanthonyssus proechimys</i>		+
<i>Lepidodorsum tiptoni</i>		+
Metastigmata		
Argasidae ^e		
<i>Ornithodoros azteci</i>		+
<i>Ornithodoros puertoricensis</i>		+
<i>Ornithodoros talaje</i>		+
<i>Ornithodoros</i> sp.		+
Ixodidae ^e		
<i>Amblyomma ovale</i>	+	+
<i>Amblyomma</i> sp.	++	++
<i>Ixodes luciae</i>	+	+
<i>Ixodes venezuelensis</i>	+	
Prostigmata		
Trombiculidae ^f		
<i>Aitkenius ciscunctatus</i>		+
<i>Atelepalme smarma</i>		+
<i>Boshkerria punctata</i>		+
<i>Crotiscus desdentatus</i>		+
<i>Eutrombicula alfreddugesi</i>	+	+
<i>Eutrombicula batatas</i>	+	+
<i>Eutrombicula goeldii</i>	+	+
<i>Eutrombicula tropica</i>		+
<i>Leptotrombidium panamensis</i>	+	

TABLE 29—(Continued)

Taxa	Occurrence ^a	
	Pan- ama	Vene- zuela
<i>Neoschoengastia americana</i>		+
<i>Odontocarus tubercularis</i> ^g	+	+
<i>Parasecia longicalcar</i>		+
<i>Parasecia manueli</i>		+
<i>Pseudoschoengastia bulbifera</i>	+	
<i>Quadrasetta antillarum</i>		+
<i>Quadrasetta flochi</i>		+
<i>Quadrasetta</i> sp.		+
INSECTA		
Anoplura ^h		
Hemiptera		
Hemiptera		
<i>Fahrenholzia hertigi</i>	+	
<i>Fahrenholzia schwartzi</i>		+
<i>Hoplopleura nesoryzomydis</i>	++	++
Siphonaptera ⁱ		
Pulicidae		
<i>Pulex simulans</i>		+
<i>Ctenocephalides felis</i>		+
Rhopalopsyllidae		
<i>Polygenis bohlsi</i>		+
<i>Polygenis dunni</i>	+	+
<i>Polygenis klagesi</i>	+	+
<i>Polygenis roberti</i>	+	+
<i>Rhopalopsyllus australis</i>	+	
<i>Rhopalopsyllus lugubris</i>	+	
Hystrichopsyllidae		
<i>Adoropsylla antiquorum</i>		+

^a Occasionally present (+) or common (++).

^b See Tipton et al. (1966) and Furman (1972).

^c Recorded as *Haemoaelaps glasgowi* by Tipton et al. (1966).

^d See Yunker and Radovsky (1966) and Saunders (1975).

^e See Fairchild et al. (1966) and Jones et al. (1972).

^f See Brennan and Yunker (1966) and Brennan and Reed (1975).

^g Recorded as *O. fieldi* by Brennan and Yunker (1966).

^h See Wenzel and Johnson (1966) and Johnson (1972).

ⁱ See Tipton and Mendez (1966) and Tipton and Machado-Allison (1972).

are promiscuous in their host associations (many of the ticks and chiggers, for example, also occur on birds and reptiles). By contrast, macronyssid and laelapid mites, and fleas of the genus *Polygenis* that infest *Z. brevicauda*

commonly parasitize just a few other taxa of small lowland mammals: murine opossums (usually *Monodelphis brevicaudata*), heteromyids (species of *Heteromys* and *Liomys*), muroids (usually *Akodon urichi*, oryzomyines, or species of *Sigmodon*), and echimyids (usually *Proechimys* species).

DISCUSSION

Zygodontomys brevicauda is nocturnal, terrestrial, consumes both animal and vegetable tissues, and appears to reproduce continuously even in seasonal environments. The species is numerically abundant in most of the lowland habitats where it occurs, including a diversity of natural and anthropogenic nonforest plant communities on the Central and South American mainland but also rain forests on some continental-shelf islands. While not conspicuously specialized to exploit unusual habitats or trophic niches, *Z. brevicauda* is nevertheless ecologically distinctive.

Zygodontomys brevicauda is perhaps best characterized as a colonist of ephemeral or temporally unstable habitats, especially of the dense herbaceous vegetation that such environments usually support. Examples of ephemeral environments are those resulting from human activities that destroy the natural climax vegetation; deforestation of the Neotropical lowlands, for example, creates grasslands and patches of shrubby secondary vegetation that would revert again to forests if left undisturbed. Temporally unstable (but not ephemeral) habitats are represented by those in the Llanos subject to flooding and drought, or other natural grasslands periodically swept by fires.

Prior to widespread human colonization of the Neotropical lowlands, savannas were probably the principal habitat of mainland populations of *Zygodontomys brevicauda*. Most Neotropical savannas are seasonal environments with fluctuating abiotic conditions that are reasonably well documented (Sarmiento, 1984) but whose consequences for resident vertebrate populations are largely unknown. The pioneering studies of Soriano (1977; cited by O'Connell, 1989), O'Connell (1981, 1989), and Vivas (1984), however, suggest that some species of small savanna mammals persist by an ability to repeatedly

abandon and reinvade local habitats in response to ambient physical conditions and resource availability. For such species, anthropogenic plant communities may resemble seasonal savanna habitats by providing unsustained episodes of resource abundance followed by deteriorating conditions that render the environment uninhabitable. The ability of tropical savanna muroids to invade croplands and other manmade habitats has been attributed to reproductive attributes that confer high intrinsic rates of population increase (Fleming, 1975; Happold, 1983), but similarities in food resources and phytophysiology between savannas and the weedy habitats created by human activities may be equally important factors.

The lowland distribution of *Zygodontomys* does not reflect an absence of nonforest habitats at higher elevations. Tate (1939) remarked that the upper limit of *Z. brevicauda* in the mountains of southern Venezuela was "about 4500 ft" (1385 m) despite the fact that the savannas in which he collected extend to at least 5200 ft (1600 m) on Mt. Roraima.¹⁰ Pastures and weedy secondary vegetation around human settlements extend continuously from near sea level to several thousand meters elevation in many parts of Colombia and western Venezuela, including areas intensively collected by the Smithsonian Venezuelan Project (Handley, 1976) which obtained no specimens of *Z. brevicauda* above 1260 m. The altitudinal distribution of *Zygodontomys* species is perhaps limited by their thermal metabolism.

¹⁰ Tate's (1932a) description of the altitudinal zonation of plants and animals on Mt. Roraima contains misleading information about *Zygodontomys*. All of the specimens of *Zygodontomys* that Tate collected in the vicinity of Roraima were taken at Arabopó (also spelled "Arabupu") and Paulo between 4000 and 4200 ft. The specimens of "*Zygodontomys*" that Tate (1932a) reported from Philipp Camp at 5200 ft were misidentified; they are *Akodon* (of an undetermined species), and were subsequently referred by Tate (1939) to *Chalcomys aerosus*. The "*Zygodontomys*" that Tate (1932a) reported from Rondon Camp at 6900 ft are inexplicable since the only rodents from that locality in the AMNH collections are *Rhipidomys macconnelli* and *Proechimys hoplomysoides* (recorded by Tate, 1939, as *Thomasomys macconnelli* and *P. cayennensis hoplomysoides*), neither of which could possibly have been mistaken, even in the heat of fieldwork, for *Zygodontomys*.

The restriction of *Zygodontomys* to non-forest habitats on the Central and South American mainland is not easily explained. Unlike savannas, rain forests are temporally stable environments that are dominated by woody plants and lack an herbaceous ground cover. The presence of *Z. brevicauda* in rain forests on Tobago, however, suggests that these ecological differences do not themselves prevent the establishment of viable sylvan populations. Perhaps significant is the impoverished rodent fauna of Tobago, which apparently lacks representatives of *Oryzomys*, *Proechimys*, and other genera that always inhabit rain forests on the Venezuelan

mainland. Conceivably, Tobagoan rain forests could be more hospitable to *Zygodontomys* than continental forests due to relaxed interspecific competition. However, *Z. brevicauda* also occurs in rain forests on Trinidad where *Oryzomys capito*, *Proechimys trinitatis*, and additional rodent species absent from Tobago are present (Worth et al., 1968). Lacking relevant data, it is pointless to speculate further concerning causal factors, but the exclusion of *Zygodontomys* from continental rainforest faunas is a fact of biogeographic importance and merits the attention of future field research.

BIOGEOGRAPHY

The climax vegetation of the lowlands throughout much of eastern Central America and northern South America is rain forest, but local precipitation and edaphic factors are responsible for a variety of open plant formations that also occur naturally in the region. Such unforested habitats are host to a characteristic vertebrate fauna whose avian, reptilian, and amphibian elements have been the subjects of at least preliminary zoogeographic accounts by Haffer (1967), Müller (1973), Hoogmoed (1979), and Rivero-Blanco and Dixon (1979). *Zygodontomys* and several other mammalian taxa are also members of this nonforest fauna, but their distributions have received scant attention in the literature. This section introduces the principal natural areas of nonforest lowland vegetation in eastern Central America and northern South America, reviews what is known concerning paleoclimates that may have affected the pre-Recent extent of nonforest habitats in the region, and describes patterns of nonforest mammalian distributions that invite causal explanation in terms of dispersal or vicariance. Suggestions for future research are provided in a concluding discussion that also considers information from other vertebrate groups.

NONFOREST VEGETATION IN THE NORTHERN NEOTROPICS

The term "nonforest vegetation" is employed herein to include a broad range of

lowland plant communities such as cactus deserts, thornscrub, savannas on well-drained or seasonally inundated soils, xerophytic woodlands, and evergreen or deciduous shrublands. Despite considerable physiognomic and floristic heterogeneity, such open habitats share many vertebrate taxa in common that are absent from intervening areas of closed-canopy forests. "Nonforest vegetation" is therefore a concept of interest chiefly to zoogeographers and seldom occurs in the phytogeographic literature from which most of the information summarized below is extracted.

The areas of nonforest lowland vegetation mapped in figure 38 are those believed to be of natural origin, at least in part. Human activities have greatly enlarged the extent of open habitats in the last century and, in some regions, widespread deforestation may date to pre-Columbian times (Bennett, 1968). In consequence, the natural boundaries between savanna and forest have often been obliterated and the original limits of some enclaves of nonforest vegetation are necessarily conjectural where edaphic, climatic, or historical information is insufficient to reconstruct them. Another impediment to accurate mapping, even where little or no human intervention has altered the landscape, is the inconsistency among published phytogeographic sources (e.g., compare the distribution of savannas in southern Surinam as depicted by Donselaar, 1969, and by Hueck, 1972). When different accounts provided

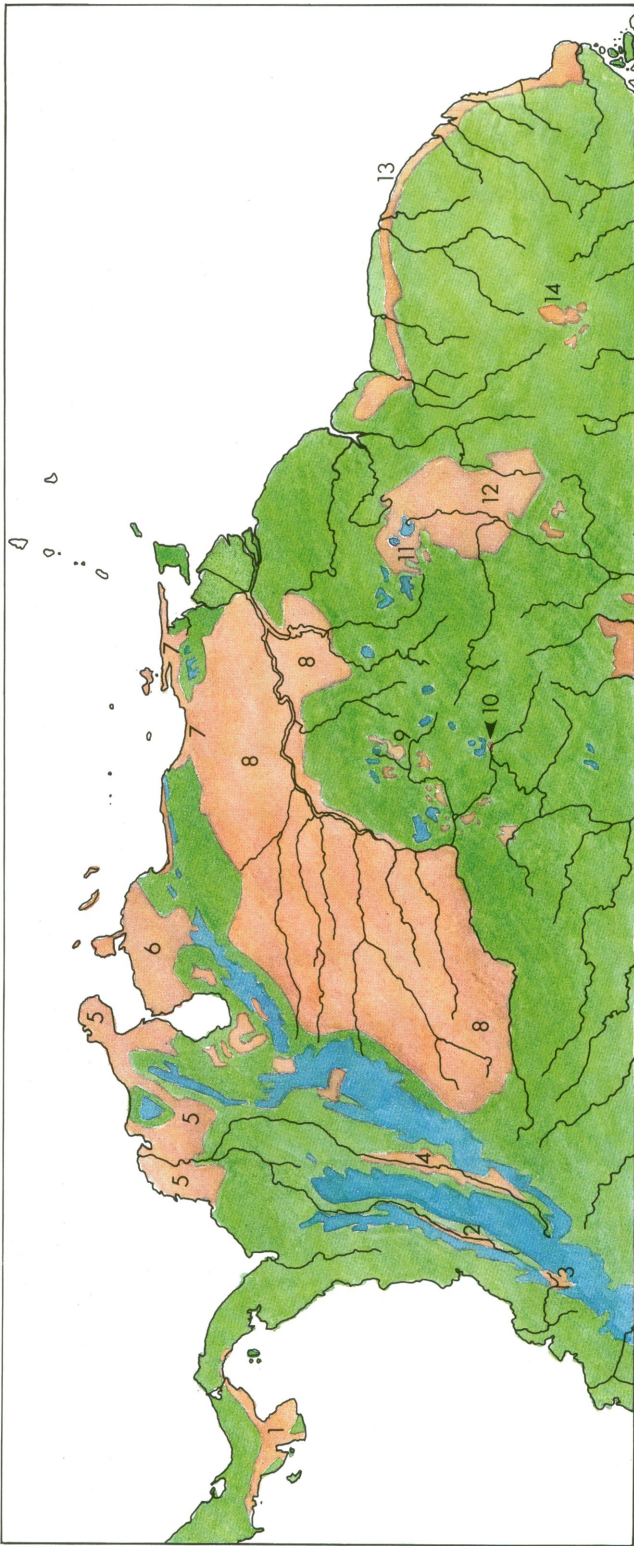


Fig. 38. Principal natural areas of unforested lowland habitats in eastern Central America and northern South America (from the equator to about 14°N). Unforested lowlands are shown in red, elevations above 1500 mm in blue; green areas are (or were until recently) forested. 1, Pacific Coast of Panama; 2, Upper Río Cauca Valley; 3, Upper Río Patía Valley; 4, Upper Río Magdalena Valley; 5, Western Caribbean Dry Zone; 6, Lara-Falcón Dry Zone; 7, Eastern Caribbean Dry Zone; 8, Llanos; 9, Ventuari Savannas; 10, Esmeralda Savannas; 11, Gran Sabana; 12, Rio Branco-Rupununi Savannas; 13, Guianan Coastal Savannas; 14, Sipaliwini-Rio Paru Savannas. (Compiled from information provided by Bennett, 1968; Espinal and Montenegro, 1963; Huber, 1982; Hueck, 1972; Pires and Prance, 1976; Sarmiento, 1976, 1983; and Donselaar, 1969.)

conflicting information about regional habitats, priority was given to maps and descriptions based on extensive first-hand experience in the field.

1. The Pacific Coast of Panama

The Caribbean lowlands of Costa Rica and Panama receive abundant rain throughout the year and are densely forested, but the Pacific lowlands of Panama experience a pronounced dry season from December to April and extensive areas west of the canal are covered by savannas or dry shrubby growth (Bennett, 1968; Porter, 1973). Some tracts of semideciduous forest, only occasionally broken by grassy clearings, occur on the western side of the Azuero Peninsula (Aldrich and Bole, 1937) but the east coast of the peninsula supports cactus and thornscrub. Much of Panama has been densely populated by humans for hundreds of years, and some of the modern nonforest vegetation is probably anthropogenic (Bennett, 1968). Panamanian grasslands are floristically similar to those of Mexico and northern South America (Sarmiento, 1983), however, so natural savanna enclaves were probably the source of colonizing plant species that spread with the progress of human deforestation. Most of eastern Panama is (or was) densely forested, but Porter (1973) reported a small savanna flora from the Darién.

2. The Upper Río Cauca Valley

3. The Upper Río Patia Valley

4. The Upper Río Magdalena Valley

The bottomlands of these intermontane valleys receive less than 2000 mm of rainfall annually and are further desiccated by cool, dry air descending the Andean slopes above them; cactus, thornscrub, grass, and xerophytic deciduous thickets form the predominant vegetation (Chapman, 1917; Espinal and Montenegro, 1963; Haffer, 1967, 1986). Other inter-Andean valleys with nonforest vegetation include those of the upper Río Dagua on the Pacific versant of the Cordillera Occidental northwest of Cali (not shown in fig. 38), the Río Chicamocha on the western slopes of the Cordillera Oriental south of Bucaramanga, the Río Zulia near Cucuta in the

southern Maracaibo Basin, and the Río Chama below Mérida in the Venezuelan Andes.

5. The Western Caribbean Dry Zone

From the Golfo de Morosquillo (about 76°W) eastward to the Guajira Peninsula and the west coast of the Golfo de Venezuela is a coastal region of cactus, thornscrub, and dry forests (Chapman, 1917; Espinal and Montenegro, 1963; Sarmiento, 1976). Semiarid conditions (500–800 mm of annual rainfall) prevail along a narrow littoral strip except for the Guajira, all of which is a desert receiving less than 500 mm of rainfall annually (Sarmiento, 1976). Contiguous with the coastal dry zone are grasslands and other open habitats that extend inland toward the confluence of the Río Cauca and the Río Magdalena, and along the valley of the Río Cesar between the Sierra Nevada de Santa Marta and the Serranía de Perijá. Much of this inland area may once have been covered by semideciduous forest (“Bosque Seco Tropical” of Espinal and Montenegro, 1963), but little continuous forest growth now remains.

6. The Lara-Falcón Dry Zone

Separated from the Western Caribbean Dry Zone by the inlet of Lake Maracaibo and the forests of the southern part of the Maracaibo Basin (which, however, include some natural savanna enclaves described by Sarmiento, 1983) is another extensive area of dry habitats. Chiefly restricted to the Venezuelan states of Lara and Falcón, this dry zone includes the southern and eastern shores of the Golfo de Venezuela, the entire Paraguaná Peninsula, and the Caribbean littoral eastward to the forested lowlands near the mouth of the Río Tocuyo; xerophytic vegetation also extends inland throughout most of the low mountains and valley systems of the upper Río Tocuyo catchment (Sarmiento, 1976). The adjacent continental-shelf island of Aruba is covered with dry vegetation as are the oceanic islands of Curaçao and Bonaire. A narrow coastal strip of dry habitats, separated from the Lara-Falcón Dry Zone by the forested lowlands of the lower Río Tocuyo, the Río Aroa, and the Río Yaracuy, extends from

the south shore of the Golfo Triste eastward to about the longitude of Caracas.

7. The Eastern Caribbean Dry Zone

Thornscrub and other kinds of dry vegetation are also encountered in the Río Unare drainage and along the eastern Caribbean coast, including the Araya Peninsula and some littoral areas of the Paria Peninsula. At the southern limits of the Río Unare drainage, this zone is contiguous with the Llanos. Rain forests flanking the coastal sierra of Sucre and swamp forests on the west coast of the Golfo de Paria limit these open habitats to the south and east. Low-lying areas on the continental-shelf island of Margarita, north of the Araya Peninsula, are also covered by xerophytic vegetation.

8. The Llanos

Encompassing an area of approximately 500,000 km², the Llanos of the Orinoco represent the largest expanse of savanna landscapes in northern South America. The Llanos are bounded by the Andes to the west and by the Cordillera de Mérida to the northwest. In the south, savannas extend to the Río Guaviare and, along the right bank of the Orinoco, Llanoan habitats reach their southeastern limits along the forested hills of the Guiana Shield. Most of the Llanos consists of open savanna or savanna woodlands growing on Quaternary alluvial and aeolian sediments, but an area of Tertiary shales and clays extending south from the coastal cordilleras of Venezuela once supported extensive semideciduous forests. Annual rainfall ranges from about 1000 mm in the northeast to about 2000 mm in the southwest. Much of the lower Llanos (below 100 m elevation) is seasonally inundated. Descriptions of Llanoan habitats and an introduction to the extensive literature on Llanoan ecology are provided by Beard (1953), Blydenstein (1967), and Sarmiento (1983).

9. The Ventuari Savannas

10. The Esmeralda Savannas

South of the Llanos is the hylaea, the vast lowland rain forests of the Orinoco and Amazon basins. Scattered across this sea of for-

ests, however, is a complex archipelago of isolated savanna enclaves of which those in the Territorio Federal Amazonas of Venezuela have received the most attention from phytogeographers and zoological collectors. Savannas near San Juan Manapiare on the Río Ventuari and those near Esmeralda on the upper Orinoco are described by Eden (1974) and Huber (1982).

11. The Gran Sabana

12. The Río Branco-Rupununi Savannas

Southeast of the Llanos and separated from them by the lowland rain forests of the Río Cuyuní and the lower Río Caroní is an undulating tableland covered by a mosaic of savannas, forests, and evergreen shrublands. Elevations range from about 1500 m near Cerro Venamo in the north to about 600 m near the Brazilian frontier. The term "Gran Sabana" is applied to these elevated savanna landscapes drained by the Río Caroní in Venezuela, but the savannas of the Rupununi-Río Branco lowlands in Guyana and Brazil are contiguous and part of the same complex (Sarmiento, 1983). The grasslands of the Gran Sabana and the Rupununi-Río Branco complex were described by Myers (1936) and Beard (1953). A general account of the vegetation of the Río Caroní basin by Huber (1986) treats the grasslands and evergreen shrublands of the Gran Sabana and the shrublands are described in additional detail by Huber (1989).

13. The Guianan Coastal Savannas

A belt of savannas extends along the Atlantic lowlands of Guyana (east of the Essequibo River), Surinam, French Guiana, and the Brazilian state of Amapá. Most of these grasslands grow on a discontinuous strip of sandy alluvium between littoral mangrove swamps and the rain forests of the interior. Since the entire region receives over 2000 mm of annual rainfall and lacks a well-defined dry season, edaphic factors are presumed responsible for these nonforest habitats. Cooper (1979) and Sarmiento (1983) provided summaries of the extensive literature on the coastal Guianan savannas; Azevedo (1967) described the little-known grasslands of Amapá.

14. The Sipaliwini-Rio Paru Savannas

A large enclave of savanna vegetation occurs in the adjacent headwaters of the Sipaliwini River (of Surinam) and the Rio Paru do Oeste (of Brazil) at elevations between about 200 and 400 m. An account of the floristics and general character of these savannas on the Surinam side was given by Donselaar (1969).

Other Brazilian Nonforest Areas

In addition to the Rupununi-Rio Branco savannas, the coastal savannas of Amapa, and the Sipaliwini-Rio Paru savannas described above, other areas of nonforest vegetation are scattered throughout the Brazilian hylaea north of the Amazon. These include both *terra firme* savannas (i.e., those not periodically flooded by river waters) known as *campos*, seasonally inundated savannas known as *campos de varzea*, and a series of vegetation formations on white sand (known as *campina*, *campinarana*, or Amazonian *caatinga*) that range in physiognomy from grasslands to low forest (Anderson, 1981). In fact, the nonforest vegetation of Brazilian Amazonia is remarkably diverse (see Pires and Prance, 1985; and Prance, 1987, for useful introductions), but little information about associated vertebrate faunas is available in the literature.

SAVANNA ECOLOGY AND QUATERNARY CLIMATES

The present geographical distribution of natural nonforest vegetation in the northern Neotropics has attracted the interest of many phytogeographers and plant ecologists. Some nonforest vegetation types are clearly correlated with climatic factors, an example being the occurrence of cactus deserts and thornscrub along the arid Caribbean coastline of Colombia and Venezuela (Sarmiento, 1976). Other nonforest plant communities are obviously restricted to peculiar soil types, such as the white-sand floras of Amazonia and the Guianas (Cooper, 1979; Anderson, 1981). Savannas are by far the most important nonforest vegetation formations in the Neotropical lowlands, however, and their ecological determinants are more complex.

The "savanna problem" of phytogeographers and ecologists is posed by the observation that climatological factors alone are insufficient to completely explain the distribution of this vegetation type. Savannas do not occur in regions with annual rainfall that is less than about 800 mm, but above this threshold savannas can be found in areas with highly seasonal or aseasonal precipitation schedules, and with annual rainfall in excess of 3000 mm (Sarmiento and Monasterio, 1975; Sarmiento, 1984; Huber, 1987). Since savannas and rain forests occur side-by-side under the same climate and on apparently similar soils in some areas, such as the Gran Sabana of Venezuela, the question of causation is puzzling.

Most Neotropical savannas do, in fact, occur under a climatic regime characterized by pronounced wet-dry seasonality; typically, the annual rainfall in savannas averages 1000 to 2000 mm, of which 80 to 90 percent occurs in a wet season five to eight months long. This is Koeppen's type Aw climate, and its distribution in tropical South America coincides with the largest regions of natural savanna vegetation (Sarmiento and Monasterio, 1975: fig. 6-2). Edaphic factors, however, especially soil nutrient deficiencies, may chiefly determine the occurrence of savannas in regions with very wet and relatively aseasonal climates. Savanna vegetation in such regions is usually not extensive but occurs in patches, typically on white sands or on old and very leached "latosols" (Sarmiento and Monasterio, 1975). In the Gran Sabana, the vegetational mosaic is unstable and savannas are spreading as a consequence of repeated burning along the margins of rain forests growing on highly acidic soils of extraordinary nutrient poverty (Folster, 1986). Recent syntheses (Sarmiento, 1984) and reviews (Huber, 1987) of Neotropical savanna research emphasize complex interactions of precipitation, fire, soil chemistry, and soil water balance as local determinants of forest-savanna dynamics, but the conspicuous macrogeographic correlation between Aw climates and savannas is compelling evidence that the amount and temporal pattern of precipitation is a major determinant of the large-scale distribution of tropical forests and grasslands.

Evidence of Quaternary climatic changes in northern South America was recently summarized by Schubert (1988). Geomorphological, sedimentological, pedological, and palynological data from many localities provide consistent evidence of widespread aridity in the late Pleistocene, probably coincident with the last glacial maximum about 18,000 years before the present (bp). Radiocarbon dates from lake sediments in northern Venezuela (Salgado-Laboriau, 1980) and from paleosols underlying fossil dunes in the llanos (Roa, 1979) suggest that arid conditions persisted in the lowlands until about 11,000 years bp. Schubert (1988: 135) concluded that, throughout northern South America and the Caribbean in the late Pleistocene, "... there existed a tropical savanna climate, with alternating yearly humid and arid phases."

Unfortunately, only a few fossil pollen sequences are available to document Pleistocene changes in the lowland vegetation of tropical South America (by contrast, Pleistocene changes in the montane vegetation are abundantly documented by pollen sequences; see Van der Hammen, 1974, for an authoritative review). One lowland pollen sequence accompanied by radiocarbon dates of Pleistocene age was obtained in the coastal plain of Guyana (Van der Hammen, 1963) and records the local dominance of savanna grasses sometime between 45,000 and 8600 years bp, presumably during the last glacial maximum; earlier and subsequent pollen samples in the sequence are dominated by mangrove-forest tree species, which are interpreted to indicate elevated sea levels during the Last Interglacial and early Recent, respectively. Another fossil pollen flora, from lake sediments in the Rupununi region of interior Guyana, has radiocarbon dates of about 7300 and 6000 bp years in the upper part of the sequence; beneath these dated sections were samples that Wijmstra and Van der Hammen (1966) believed to document an expansion of savanna grasslands (replacing woodlands) coincident with lower water levels between 13,000 and 10,000 years bp (these latter dates were obtained by extrapolation from estimated sedimentation rates). Unfortunately, because both the coastal and interior regions of Guyana support savannas at the present time, these two sequences provide no evidence that

open vegetation actually replaced rain forests in the northern Neotropics. In fact, the only definite indication of pre-Recent savannas in an area of lowland South America now covered by rain forests derives from palynological analyses of a small series of bore-hole samples collected in the Brazilian state of Rondonia (Van der Hammen, 1972; Absy and Van der Hammen, 1976). Holocene pollen records from Amazonia (e.g., those reported by Absy, 1982, 1985; and Liu and Colinvaux, 1988) document several episodes of reduced precipitation during the last 6000 years, but none are believed to have been severe enough to have caused major expansions of savannas or other nonforest habitats.

In summary, there is abundant evidence of late Pleistocene aridity across much of the northern Neotropics, but (as yet) scant documentation from the fossil pollen record of savannas or other open vegetation formations in regions now covered by forests. Nevertheless, the disjunct ranges of many plant and animal taxa across northern South America have prompted some biogeographers to conclude that open habitats were once continuous in the region, and that modern savanna enclaves with their isolated faunas are the vicariant relicts of post-Pleistocene expansions of the rain forest. The distribution of nonforest mammals has yet to be considered from this historical perspective.

THE NONFOREST MAMMAL FAUNA

Many species of mammals inhabit open vegetation formations in northern South America, but only a few appear to be entirely restricted to nonforest habitats. Most of the larger mammals that populate savannas, for example, also occur throughout the rain forests of Amazonia (e.g., *Myrmecophaga tridactyla*, *Tamandua tetradactyla*, *Cabassous unicinctus*, *Dasyus novemcinctus*, *Priodontes maximus*, *Felis yagouaroundi*, and *Tayassu tajacu*; see Emmons and Feer, 1990). Other species, although most abundant in open vegetation, are also occasionally collected in lowland or montane forests (e.g., *Cerdocyon thous*, *Conepatus semistriatus*, and *Odocoileus virginianus*; see Handley, 1976). Several semiaquatic species appear to occur

TABLE 30
Distribution of Nine Nonforest Mammalian Taxa in the Northern Neotropics

Nonforest taxa	Nonforest areas ^a														Sources ^b
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
MARSUPIALIA															
Didelphidae															
<i>Lutreolina crassicaudata</i>								X			X		X		1, 2, 3
EDENTATA															
Dasypodidae															
<i>Dasypus sabanicola</i>					X			X							4, 5
RODENTIA															
Muridae															
<i>Calomys hummelincki</i>					X	X		X							6, 7
<i>Sigmodon alstoni</i>					X	X	X	X	X		X	X	X	X	6, 8, 9, 10
<i>S. hispidus</i>	X	?	?	X	X	X		X							6, 11, 12
<i>Zygodontomys brevicauda</i>	X			X	X	X	X	X	X	X	X	X	X	X	13
<i>Z. brunneus</i>		X	X	X											13
Caviidae															
<i>Cavia aperea</i>								X			X	X	X	X	6, 8, 14, 15, 16
LAGOMORPHA															
Leporidae															
<i>Sylvilagus floridanus</i>				X	X	X	X	X							17, 18

^a Numbered nonforest areas are mapped in figure 38 and described in the text.

^b Sources: (1) Lemke et al., 1982; (2) Pérez-Hernández, 1989; (3) specimen in MHNLS; (4) Wetzel and Mondolfi, 1979; (5) Ayarzagüena, 1982; (6) Handley, 1976; (7) Petter and Baud, 1981; (8) Husson, 1978; (9) Williams et al., 1983; (10) specimens in AMNH and FMNH; (11) Handley, 1966; (12) specimens in AMNH and USNM; (13) this report; (14) Thomas, 1901; (15) Tate, 1939; (16) specimens in AMNH, MHNLS, ROM, USNM, and UVM; (17) Hershkovitz, 1950; (18) this report, Appendix 3.

indifferently in forests or savannas, wherever suitable aqueous environments are present (e.g., *Pteronura brasiliensis*, *Holochilus brasiliensis*, and *Hydrochaeris hydrochaeris*). A few small species found in savanna regions are arboreal, living in gallery forests or tree islands surrounded by grasslands, and are not really part of the nonforest fauna (e.g., *Marmosa robinsoni* and *Oecomys speciosus*). Finally, some nominal species inhabit open vegetation in some regions but rain forests in others (*Akodon "urichi"* and *Oligoryzomys "fulvescens"* are conspicuous examples); revisionary studies may demonstrate that such anomalous ecological distributions actually involve two or more cryptic species.

Information gathered from collection records, manuscript fieldnotes, and published reports suggests that just nine species of non-volant small mammals from the lowlands of northern South America are so closely restricted to open habitats with an herbaceous

ground cover that they rarely or never penetrate closed-canopy forests (table 30). The nature of the evidence for classifying each as a nonforest species is summarized below, excepting the species of *Zygodontomys* for which habitat information was provided earlier.

***Lutreolina crassicaudata*:** This opossum has been taken at only eight localities in northern South America (Lemke et al., 1982; Pérez-Hernández, 1989), all in regions below about 900 m elevation with apparently natural savanna vegetation. Four specimens, reported by Handley (1976) from Llanoan savannas south of the Orinoco, were taken in grass; Lemke et al. (1982) reported seven collected in "low marshes" and one in "open savanna" in the Colombian Llanos. Two unpublished specimens, collected near San Ignacio Yuruaní in the Gran Sabana (one is MHNLS 8080, taken in the course of our 1987 fieldwork), were captured in dense grass. South of the Amazon, *L. crassicaudata* is widely

distributed in savannas and temperate grasslands (Marshall, 1978). Mares (1981) reported two specimens from "subtropical Moist Forest" in Provincia Salta, Argentina, but I know of no collection records from tropical rain forests.

***Dasypus sabanicola*:** Since its scientific discovery in 1967, this small armadillo has been collected throughout the Llanos of Colombia and Venezuela where it appears to occur exclusively in grassy savanna habitats (Mondolfi, 1968; Handley, 1976; Ojasti, 1981; Ayarzagüena, 1982). A single specimen from the upper Río Magdalena valley in Colombia (Wetzel and Mondolfi, 1979) is the only record from any area other than the Llanos. All of the localities where this species is known to occur are several hundred meters or less in elevation.

***Calomys hummelincki*:** This tiny mouse is known from five localities in the Venezuelan Llanos and the Lara-Falcón Dry Zone reported by Butterworth (1960) and Handley (1976), and from a single specimen collected on the Guajira Peninsula (Petter and Baud, 1981); two additional localities in the Venezuelan Llanos are documented by unpublished specimens (MHNLS 4906 and 5781). All of these collection records are from unforested regions below about 200 m elevation. Butterworth (1960) found four specimens under trash and boards in an oil-prospecting camp, and six in an adjacent "marshy meadow." Data from 44 specimens summarized by Handley (1976: 53) are the only other ecological observations available from mainland populations: 42 specimens were taken in "sandy grasslands," one in "thorn forest," and one in a "yard." *C. hummelincki* also occurs on the desert islands of Aruba and Curaçao (from which Husson, 1960, described it as a species of *Baiomys*), and it is known from fossils on Tobago (Eshelman and Morgan, 1985).

***Sigmodon alstoni* and *S. hispidus*:** These rats are known from hundreds of specimens and dozens of collection localities in Colombia, Venezuela, the Guianas, and northern Brazil (Ecuadorean and Peruvian populations belong to other species, *S. inopinatus* and *S. peruanus*). Handley (1976) summarized habitat data from 140 specimens of *S. alstoni* and 326 specimens of *S. hispidus* col-

lected in Venezuela: all were taken in grasslands or in disturbed, secondary vegetation associated with human habitations and agriculture. Other reports (e.g., Osgood, 1912; Tate, 1939; Handley, 1966; Husson, 1978; Williams et al., 1983; and Vivas, 1986) consistently describe collections of these species from savannas and other open habitats. Fleming (1970) reported that *S. hispidus* invaded a Panamanian semideciduous dry forest along the grassy margins of paved roads, but I know of no record of either species from undisturbed, closed-canopy tropical forests of any kind. My compilation of data from 43 localities where *S. alstoni* has been collected indicates an altitudinal distribution from sea level to about 1300 m. Forty-six South American localities from which I have recorded data for *S. hispidus* range from sea level to about 2000 m, but most (93%) are less than 1300 m elevation.

Cuervo-Díaz et al. (1986) recorded *S. hispidus* from the Cauca and Patia valleys of Colombia, but I have not seen any specimens from those areas and the species is not recorded in Alberico's (1983) list of the mammals of the Departamento del Valle.

***Cavia aperea*:** This account follows Hückinghaus's (1961) revision of the subfamily Caviinae by treating all of the wild populations of caviés in northern South America east of the Andes as conspecific with *aperea* Erxleben 1777 from Pernambuco, and by reserving *porcellus* Linnaeus 1758 for the domesticated guinea pig. There is little consensus on *Cavia* taxonomy in the literature, however, and future revisionary studies may discover that more than one species occurs in the area, or that other names apply to them.

Caviés are widespread in the Llanos of Colombia, but their distribution in Venezuela appears to be spotty and they have rarely been collected in the Guianas. Almost all specimens have been taken in savannas, fallow agricultural areas, and other open, grassy habitats (Tate, 1939; Ojasti, 1964; Handley, 1976; Williams et al., 1983); our specimens from San Ignacio (table 23) were trapped in dense grass. Twenty-one collection localities east of the Andes (representing the nominal species-group taxa *caripensis*, *guianae*, and *venezuelensis*) range from sea level to about 1200 m elevation. Caviés from the eastern

Andes of Colombia (mostly near Bogota) represent the nominal species *anolaimae* and range from about 1500 to at least 2500 m elevation.

Sylvilagus floridanus: Cottontails inhabit deserts, thornscrub, open woodlands, and savannas in Colombia, Venezuela, and some offshore islands (Osgood, 1912; Hershkovitz, 1950; Handley, 1976; Ojeda and Keith, 1982). Chapman et al. (1980) claimed that *S. floridanus* has "historically" occurred in rain forests, but they cite no evidence and I am unaware of a single such record; instead, the rainforest rabbit throughout Central and South America is the tapití, *S. brasiliensis* (Hershkovitz, 1950; Handley, 1976; Emmons and Feer, 1990). Cuervo-Díaz et al. (1986) reported that *S. floridanus* extends its altitudinal range to about 2100 m in Colombia, but provided no information about specimens or localities. The highest elevation from which I have examined a South American specimen is 1400 m (MHNLS 5, from "La Sierra," Edo. Cojedes, Venezuela); all other records (totaling 357 specimens from 83 localities) are from 1000 m or less.

DISCUSSION

The nonforest mammals listed in table 30 include representatives of lineages that have long evolutionary histories in South America, since at least the Cretaceous (didelphid marsupials), the Paleocene (dasypodid edentates), or the Oligocene (caviomorph rodents), together with one species of a genus (*Sylvilagus*) that is probably a Pleistocene immigrant from North America (see Patterson and Pascual, 1972, for an authoritative synopsis of the South American fossil record). The remaining taxa are muroid rodents, a group whose antiquity in South America is controversial (Webb, 1985; Voss, 1988). Despite such diverse origins, this is an ecologically distinctive fauna that merits biogeographic analysis. However, two preliminary caveats regarding the data are in order.

1. Some of these animals are so infrequently collected, even in regions where they are known to occur, that the lack of specimens from other areas cannot be assumed to indicate that the species are absent there. *Lutreolina crassicaudata*, *Dasypus sabanicola*,

Calomys hummelincki, and *Cavia aperea* are difficult to collect unless special efforts are made, and their distributions among the un-forested regions of northern South America may therefore be more extensive than those indicated in table 30.

2. Some of the tabulated nonforest areas have seldom been visited by mammalogical collectors and few have been sampled intensively or often enough that the whole fauna can be assumed to be known. The Pacific lowlands of Panama (area 1) and the Llanos (area 8) are perhaps the best sampled of the regions under consideration, followed by the Caribbean dry zones of Colombia and Venezuela (areas 5, 6, and 7), the Gran Sabana (area 11), the Rio Branco-Rupununi savannas (area 12), and the Guianan coastal savannas (area 13). It is much more difficult to evaluate the mammal faunas of the dry intermontane valleys of Colombia (areas 2, 3, and 4), the isolated savannas of Amazonian Venezuela (areas 9 and 10), and the Sipaliwini-Rio Paru savannas (area 14) since collections from these regions are rudimentary at best.

ENDEMISM AND DIVERSITY: *Zygodontomys* is the only genus of nonforest mammals endemic to eastern Central America and northern South America, but three nonforest mammalian species are also endemic to the region: *Dasypus sabanicola*, *Calomys hummelincki*, and *Sigmodon alstoni*. This small roster is unimpressive by comparison with the mammalian endemism of trans-Amazonian nonforest areas (e.g., the cerrado, caatinga, pantanal, and chaco) but does provide evidence that the northern savannas are not exclusively populated by undifferentiated immigrants.

Of the faunas tabulated, that of the Llanos is by far the most diverse, including eight of the nine nonforest species considered in this report. Most Llanoan species occur in the grasslands extending along the right bank of the Orinoco from the vicinity of Puerto Ayacucho (ca. 67°30'W) to around the mouth of the Río Caroní (ca. 62°40'W), but isolated savanna areas to the south and east appear to be depauperate: *Dasypus sabanicola*, *Calomys hummelincki*, and *Sylvilagus floridanus* are unknown from the Gran Sabana and the Rio Branco-Rupununi savannas. (Other

Llanoan, but not strictly nonforest, taxa that likewise do not occur in these areas include the skunk *Conepatus semistriatus* and the fox *Urocyon cinereoargenteus*; Bisbal, 1989.)

Northwest of the Llanos, the Western Caribbean and Lara-Falcón Dry Zones appear to support less diverse nonforest faunas, but the missing taxa (*Lutreolina crassicaudata*, *Dasytus sabanicola*, and *Cavia aperea*) are cryptic or elusive and might yet be found to occur there. By contrast, the well-sampled Pacific lowlands of Panama are clearly impoverished: of the nonforest species considered here, only *Sigmodon hispidus* and *Zygodontomys brevicauda* are known to occur in eastern Central America.

Due to inadequate sampling it is difficult to assess the diversity of nonforest mammals in the intermontane valleys of Colombia, the Amazonian savannas of Venezuela, and the Sipaliwini-Rio Paru savannas. Future collecting expeditions to these regions should attempt to determine whether nonforest species known from other areas occur there as well.

FAUNAL RELATIONSHIPS: Of the nonforest species that are not endemic to eastern Central America and northern South America, two exhibit range disjunctions across the Amazonian hylaea. *Lutreolina crassicaudata* and *Cavia aperea*, as currently recognized, each include populations in the northern savannas and in the unforest lowlands of southern Brazil, Paraguay, eastern Bolivia, northern Argentina, and Uruguay. Neither *Lutreolina* (which is monotypic) nor *Cavia* occurs in Central America. Other species of *Cavia* occur south of the Amazon and in the Andes.

The remaining nonendemic species, *Sigmodon hispidus* and *Sylvilagus floridanus*, do not occur south of the Amazon but instead have extensive ranges in Central America and North America (Hall, 1981). In addition to *Sigmodon alstoni* (a northern savanna endemic), two other species of cotton rats occur in South America and six additional congeners are currently recognized in the North American fauna (Honacki et al., 1982). Other species of *Sylvilagus* range from northern Argentina to Canada (Hershkovitz, 1950; Hall, 1981).

The extralimital relationships of the endemic nonforest taxa are unambiguous only for *Calomys hummelincki*, all of whose congeners occur either in unforest lowland habitats south of the Amazon or in Andean grasslands and scrub (Hershkovitz, 1962). As discussed earlier in this monograph, the relationships of *Zygodontomys* are problematic and no sister taxon to this genus can be identified with confidence. The relationships of *Dasytus sabanicola* and *Sigmodon alstoni* with their respective congeners are unknown.

HISTORICAL INTERPRETATIONS: Explanations for range disjunctions of nonforest plants and animals in the tropical lowlands of South America may be classified as invoking either vicariance or dispersal. Ducke and Black's (1953) classic essay on Amazonian vegetation provided what appears to be the earliest articulate recognition of the historical-biogeographic problem:

The soil and, in the case of larger savannas, also the climate, are certainly responsible for the presence, in many parts of the hylaea, of large open areas ("campos") or small spots ("campinas") of open land, surrounded on all sides by the great virgin forest. Some authors attribute the presence of open land in the middle of the virgin forest to fire; this is however not true. Natural "campos" and "campinas", often separated by hundreds of kilometers, have a flora and fauna radically diverse from that of the neighboring forests (of either virgin or secondary growth) and with many species in common, never observed elsewhere in the same region. The true natural "campos" are grasslands inhabited by a flora foreign to the hylaea, of species widely distributed over the continent or belonging to the "cerrado" of Minas Gerais, Matto Grosso, etc. [op. cit.: p. 10]

Like "campos", the "campinas" are primary formations *probably older than the rain forest of the hylaea* [my italics]; this is indicated by the presence of many plants and animals of the same species, on many campos or campinas often separated by hundreds of kilometers of rain forest where those species do not occur. The flora of clearings sometimes called campinas, originating from the burning of the forest, is entirely different; it is composed of the same species as the common secondary growth ("capoeira"). [op. cit.: p. 43]

The presence of the same species of plants on several or many campos or campinas throughout the hylaea, separated by large extensions of rain forest, indicates a very remote origin of the flora of these open areas. However, there are similar formations apparently of recent origin . . . [such] apparently recent campos lack rattlesnakes . . . [which] are present on all true upland campos within . . . Amazonia and [are] restricted to them. [op. cit.: 45-46]

Lacking evidence for paleoclimatic fluctuations, Ducke and Black were unable to specify the mechanism by which an older, continuous savanna flora and fauna were replaced or surrounded by forests, but the scenario is clearly implied. Discoveries by geomorphologists and paleopalynologists in subsequent decades, however, were quickly incorporated in zoogeographic accounts that explicitly invoked climatically correlated late Pleistocene or early Holocene vicariance to explain the modern distribution of lowland nonforest faunas (Haffer, 1967, 1979; Hoogmoed, 1973, 1979; Müller, 1973).

By contrast with hypotheses that propose common mechanisms to explain the congruent distributions of many taxa, dispersalist interpretations of biological range disjunctions are often distinctly ad hoc. Butterworth (1960), for example, suggested that a Venezuelan population of *Calomys* "*laucha*" (= *C. hummelincki*) may have been accidentally transported from Bolivia in shipments of petroleum surveying equipment. Similarly, Hershkovitz (1972) conjectured that *Zygodontomys* and *Sigmodon* invaded the interior savannas of the Guianas from the coast "... by spreading along cleared or cultivated river banks" (p. 402), but that isolated populations of *Cavia* "... have all the characteristics of feral populations of pre-Columbian domestic stock" (p. 416). At issue here is whether independent evidence exists to support such particular explanations against alternatives that account more parsimoniously for whole faunas and floras.

Butterworth's (1960) speculation regarding *Calomys hummelincki* can be rejected categorically since the species has subsequently been found to occur widely in the Llanos and adjacent nonforest areas and is known from Pleistocene cave deposits on Tobago (see the preceding species account for details and references). Hershkovitz's (1972) suggestions concerning *Sigmodon* and *Zygodontomys*, however, are difficult to evaluate in the absence of any cited evidence for continuous aboriginal river settlements between coastal and interior savannas. Likewise, Hershkovitz did not explain how wild cavies can be recognized as descended from escaped domestic stock and, to the best of my knowledge, there

are no reports in the anthropological literature that *Cavia* species were ever widely husbanded by the lowland cultures of tropical South America.¹¹

While some dispersalist explanations thus appear to be erroneous or inadequately documented, it is obvious that vicariance and dispersal are not mutually exclusive processes since both could have contributed to the present distribution of nonforest biotas. Presumably, many of the nonforest birds listed by Haffer (1967) are capable of sustained flight over considerable expanses of rain forest, and Kubitzki (1983) has suggested that some of the plants characteristic of Amazonian savanna enclaves have diaspores adapted for transportation by wind or flying vertebrates. Thus, the plausibility of vicariance or dispersal as an explanation for any specified range disjunction must be judged in terms of the biology of the organism concerned. Geophysical and palynological evidence of Quaternary climatic fluctuations provides a causal mechanism for vicariance but does not compel the conclusion that every isolated population of nonforest plant or animal in the Neotropical lowlands is of late Pleistocene origin.

That dispersal and vicariance may have diversely affected the distribution of Neotropical nonforest vertebrates is suggested by differences in the faunal relationships of birds and mammals. Biogeographic accounts of South American lowland birds (e.g., Haffer, 1967, 1979, 1985) consistently emphasize the striking resemblance between savanna avi-faunas north and south of the Amazon. By contrast, transAmazonian comparisons of

¹¹ The authoritative *Handbook of South American Indians* contains no mention of guinea pigs husbanded by any tropical lowland tribes except the Jivaro of eastern Ecuador who were historically in contact with the Inca (Stewart, 1948). Dr. Robert Carneiro (of the AMNH Department of Anthropology) has spent a lifetime studying the tropical lowland cultures of South America and knows of no other example of guinea-pig husbandry among them (personal commun.). It is relevant to mention that the Pemón, who inhabit grasslands in southeastern Venezuela, northern Brazil, and southern Guyana where *Cavia* is locally abundant, utilize only chickens, dogs, and cattle (all postconquest acquisitions) as domesticated animals (Thomas, 1983).



Fig. 39. Nonforest areas of northern South America in relation to Amazonia and the Cerrado. Distribution of northern nonforest areas is documented by references cited in the caption to figure 38; extent of cerrado vegetation is as mapped by Hueck (1972).

savanna mammal faunas are more remarkable for the dramatic differences revealed. The most extensive savanna landscapes south of the Amazon are those of the Cerrado (fig. 39), whose nonforest muroid rodent fauna bears slight resemblance to that of the northern savannas (compare tables 30 and 31). Clearly, there is little support in these data for the uninhibited migration of "pastoral" muroid faunas across Amazonia postulated by Marshall (1979). Instead, the Amazon and its gallery forests may have formed a substantial barrier to the north-south dispersal of flightless savanna vertebrates during arid climatic episodes of the past.

A SCENARIO FOR *ZYGODONTOMYS BREVICAUDA*: The geographic patterns of morphological and ecological variation in *Zygodontomys brevicauda* described earlier in this

monograph can be accommodated in an evolutionary scenario based on the assumption that the distribution of flightless nonforest vertebrate species in northern South America is best explained by hypotheses of vicariance consistent with the paleoclimatic record.

Population-sample frequencies of carotid arterial variants (table 10) suggest that a northwestern complex of contiguous nonforest regions was separated at some early date from a southeastern nonforest complex, possibly by forests invading lowland gaps in the mountainous arc formed by the Cordillera Oriental, the Cordillera de Mérida, and the Cordillera de la Costa (fig. 24). The area relationships implied by this distribution (1, 4, 5, 6) (7, 8, 9, 10, 11, 12, 13) can be made historically explicit with assumptions concerning carotid character evolution. Al-

though the genus *Zygodontomys* lacks a well corroborated outgroup, the species *Z. brunneus* (with a complete stapedia circulation) can be employed tentatively to polarize character transformations in *Z. brevicauda*. By this comparison, the predominant stapedia morphology of the subspecies *cherriei* appears to be primitive, and it can then be surmised that nonforest areas 7, 8, 9, 10, 11, 12, and 13 (presently occupied by the subspecies *brevicauda* and *microtinus*) were contiguous more recently than any were with outlying regions. Nonforest areas not included in this hypothesis of geographic relationships are the Río Cauca and Río Patia valleys (areas 2 and 3) where *Z. brevicauda* does not occur, and the Sipaliwini-Río Paru complex (area 14) from which only a single specimen is presently available.

Although the coastal savannas of the Guianas were treated for descriptive convenience as comprising a single nonforest unit (area 13 in fig. 38), the distribution of the subspecies *microtinus* from Guyana to French Guiana is nevertheless zoogeographically significant because savanna vegetation in the region is discontinuous (as noted earlier) and the coastline is also broken up by the debouchments of large rivers (e.g., the Courantyne and Maroni). If, as suggested by outgroup comparisons with *Z. brunneus*, the complete bony roof of the mesopterygoid fossa that distinguishes *Z. brevicauda microtinus* from the nominate subspecies *brevicauda* is postulated to be derived, then these fragmented coastal habitats (together with any inland enclaves in which *microtinus* may yet be found) form a historically related subgroup within the southwestern series of nonforest areas.

Islands on the continental shelf are inhabited by morphologically and ecologically distinctive populations of *Zygodontomys brevicauda* that remain to be fit into this historical scheme. Tate (1939) grouped the nominal insular taxa then recognized from San Miguel Island (Panama) and Trinidad together with *Z. brunneus* on the basis of their large size, but the implication of phylogenetic propinquity is geographically implausible. Instead, island forms of *Z. brevicauda* resemble adjacent mainland populations in qualitative craniodental characters as would be expected

TABLE 31
Nonforest Muroid Rodents of the Cerrado^a

<i>Akodon lindberghi</i> ^b
<i>Bolomys lasiurus</i>
<i>Calomys callosus</i>
<i>Calomys tener</i>
<i>Juscelinomys candango</i>
<i>Kunsia fronto</i>
<i>Kunsia tomentosus</i>
<i>Oryzomys subflavus</i>
<i>Oxymycterus roberti</i>
<i>Pseudoryzomys simplex</i> ^c
<i>Thalpomys cerradensis</i> ^d
<i>Thalpomys lasiotis</i> ^e

^a Based on information provided by Alho et al. (1986), Redford and Fonseca (1986), Mares et al. (1989), Hershkovitz (1990a, 1990b), Voss and Myers (1991), and collections from the Serra do Roncador (Matto Grosso) in the BMNH.

^b Correct name for the species referred to by the nomen nudum *Plectomys paludicola* in the Brazilian literature (see Hershkovitz, 1990b).

^c See Voss and Myers (1991); not the species referred to by this name in the ecological literature (e.g., Redford and Fonseca, 1986).

^d "*Akodon* sp. 1" of Mares et al. (1989) according to Hershkovitz (1990a).

^e The senior synonym of *Akodon reinhardti* (see Hershkovitz, 1990a).

of recent vicariants. While it is possible that large size is an ancestral condition retained by insular plesiomorphs, an alternative explanation is that gigantism evolved convergently in response to selection correlated with island ecology.

Populations of *Zygodontomys brevicauda* on San Miguel Island, Trinidad, and Tobago differ from mainland populations by inhabiting forests (see Natural History: Summary of Habitat Information, above) and some physical or biotic aspect of sylvan environments might confer a selective advantage to larger individuals. However, insular gigantism is a widespread phenomenon in muroid rodents (Foster, 1964, 1965) as are size differences between island and mainland populations of mammals generally (see Heaney, 1978; and Lomolino, 1985, for reviews). A special explanation for insular size trends in *Z. brevicauda* therefore seems inappropriate, especially in the absence of compelling causal evidence.

The fossil record of Tobago provides a his-

torical context for one forest-dwelling island population. At the present time, *Z. brevicauda* is the only representative of the continental nonforest fauna to inhabit Tobago but, in a cave fauna that Eshelman and Morgan (1985) believed to be of late Pleistocene age, *Z. brevicauda* was found to co-occur with other nonforest species: *Calomys hummelincki*, *Sigmodon alstoni*, and possibly *Sylvilagus floridanus*. Eshelman and Morgan (1985) pointed out that since the marine seaways separating Tobago from Trinidad and the mainland are less than 100 m deep, the island was presumably connected to the continent by emergent land during the last glacial maximum. Since this connection probably coincided with an arid paleoclimate favoring savannas and other open vegetation formations (see Schubert, 1988, and the preceding discussion in this text section), Tobago was likely colonized by a nonforest mainland fauna. With rising postglacial sea levels and increased rainfall, nonforest mammals stranded on Tobago and unable to survive the ecological transformation to forest habitats presumably dwindled to extinction, with the evident exception of *Z. brevicauda*. Similar scenarios could account for other insular sylvan populations, but no relevant fossil evidence is currently available.

EVIDENCE OF AREA RELATIONSHIPS FROM OTHER SPECIES: If *Zygodontomys* shares a common history of vicariance with other nonforest vertebrates, then phylogenetic analyses of repeated patterns of speciation and population divergence should yield congruent area cladograms. Unfortunately, most zoogeographic discussions of the nonforest fauna are couched in terms of subspecific taxonomies whose historical implications are impossible to evaluate. Müller (1973: fig. 87), for example, mapped the distribution of the subspecies of *Campylorhynchus griseus*, a wren restricted to open habitats in northern South America. One subspecies (*C. g. bicolor*) inhabits the upper Río Magdalena valley, another (*C. g. albicilius*) the Western Caribbean and Lara-Falcón dry zones, a third (*C. g. minor*) occupies isolated savanna enclaves in southern Venezuela, and a fifth (*C. g. griseus*) is restricted to the Gran Sabana-Rio Branco-Rupununi savanna complex. While such in-

formation could at least be expected to indicate a measure of reproductive isolation among populations inhabiting disjunct areas of nonforest vegetation, the phenotypic differences upon which these subspecies are based are so vague as to preclude any confident genetic or historical inference:

According to Hellmayr . . . , *C. g. griseus* differs from *C. g. minor* in having the upper parts and edges of the wing coverts buffy brown rather than russet brown. Phelps and Phelps . . . [however,] reported that "the only difference between *griseus* and *minor* is the color of the back and the slight buffy tint to the underparts of the latter. The pattern of the white bands on the tail . . . is identical." In the only specimen of *C. g. griseus* that I have examined, an adult female in very worn and faded plumage . . . the dark barring of the wing coverts, edges of the rectrices, and upper tail coverts is more distinct than in specimens of *C. g. minor* examined (Selander, 1964: 41).

Another example cited by Müller (1973) to illustrate "subspeciation" in the nonforest vertebrate fauna is the rabbit *Sylvilagus floridanus*, the geographic variants of which are said to resemble those of *Campylorhynchus griseus* in distribution. In fact, the subspecies taxonomy of *S. floridanus* completely obscures the single striking geographic pattern of character variation among northern South America cottontails (fig. 40). Specimens from the Maracaibo Basin, the Paraguaná Peninsula, and the offshore islands of Aruba and Curaçao have black nuchal patches while specimens from Colombia and the Llanos have red nuchal patches; populations from intermediate regions, such as the hinterlands of the Lara-Falcón Dry Zone and deforested gaps in the divide between Caribbean and Atlantic watersheds, exhibit intermediate phenotypes. This geographic pattern is of historical interest because black napes are clearly derived (other species of *Sylvilagus* have reddish nuchal patches) and their distribution in the Maracaibo region and on the continental-shelf island of Aruba suggests a late Pleistocene land connection coincident with ecological isolation from mainland areas with red-naped rabbits. Confusingly, black-naped rabbits from Aruba and Curaçao (*S. f. nigronuchalis*) are taxonomically distinguished from mainland populations with black napes (*S. f. continentis*) and several subspecies of red-naped mainland rabbits are recognized

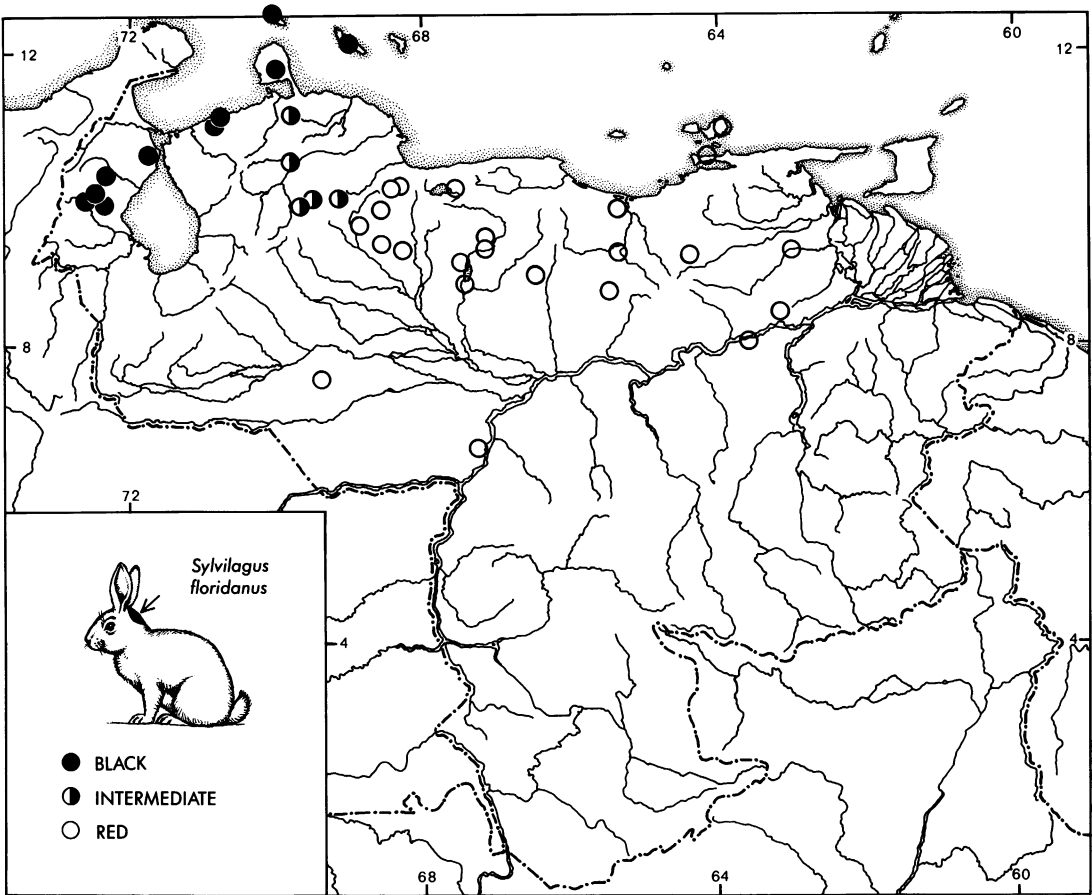


Fig. 40. Distribution of nuchal color variants of the rabbit *Sylvilagus floridanus* in Venezuela and adjacent islands. Specimen documentation is provided in Appendix 3. Smithe's (1975–1981) Sepia (color 119) and Vandyke Brown (color 121) are considered “black”; Prout's Brown (color 121A) and Brussels Brown (color 121B) are considered “intermediate”; Antique Brown (color 37), Tawny (color 38), and Cinnamon-Rufous (color 40) are considered “red.”

(Hershkovitz, 1950); most cited subspecific characters are indistinct.

Many more such examples could be provided, but the issue here is not the inutility of subspecies per se. Rather, the problem lies with the retention in the literature of inadequately diagnosed taxa dating from earlier eras of systematic practice when any difference, however slight, served as sufficient justification for a new name. Confident zoogeographic inference requires a secure basis in revisionary systematic studies, and zoogeographers should consider character variation explicitly unless well corroborated phylogenetic hypotheses are already available for

their purposes. At the present time, I am aware of no source of information about phylogenetically analyzable character variation in other members of the nonforest vertebrate fauna. Future efforts to obtain such information should focus on common species, with limited dispersal abilities, that are widely distributed among disjunct nonforest areas. Examples might include *Sylvilagus floridanus* and species of *Sigmodon*, possibly some of the smaller savanna bird species (such as *Campylorhynchus griseus*), the lizards *Cnemidophorus lemniscatus* and *Kentropyx striatus* (Hoogmoed, 1973, 1979), and the rattlesnake *Crotalus durissus* (Müller, 1973).

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APPENDIX 1

List of Measured Specimens

TABLE 5

El Dividive: USNM 372541, 372542, 372545, 372547, 372549–372554, 372556–372558, 372560, 372562–372564, 372567–372572, 372574, 372575, 372577–372588, 372590, 372592, 372599, 372601, 372602, 372605, 372607, 372609–372614, 372616–372619, 372622, 372623, 372625–372634, 372638, 372639.

TABLE 8

Caparrapi: (*brunneus*): ICN 367, 376, 388; USNM 282114. **Paime** (*brunneus*): AMNH 69177, 70527, 71233; USNM 251967, 251969, 251970. **Andalucía** (*brunneus*): AMNH 33773. **Valle de Suaza** (*brunneus*): USNM 541897–541899, 541902–541906, 541908, 541909, 541911, 541914, 541915, 541917, 541921, 541923, 541928–541935, 541938; UVM-CDB 428, 432, 450. **Hacienda Montebello** (*brunneus*): ICN 418. **Caparrapi** (*brevicauda*): ICN 384, 1865; USNM 282113. **Valle de Suaza** (*brevicauda*): USNM 541900, 541941. **Villavieja** (*brevicauda*): MVZ 113379–113383, 113951, 113952, 113954–113958, 114241. **Chicoral** (*brevicauda*): AMNH 32920. **El Triunfo** (*brevicauda*): AMNH 34592.

TABLE 9

San Jerónimo: FMNH 70187, 70188, 70192, 70193, 71095, 70199, 70202, 70205, 70208, 70227, 70229, 70232. **Hacienda Formosa:** UBV 3579, 3580, 3582–3587. **Finca Arizona:** UVB 3094–3100, 3102, 3108–3112, 3445, 3446, 3448.

TABLE 13

Bush Bush Forest: AMNH 185475, 186840, 186844, 186846, 186847, 186852, 186857, 186859, 186865, 186868, 186870–186877, 186881, 186882, 186884, 186886, 186887, 188499, 188501–188503, 188505, 188506, 188509. **Sangre Grande:** AMNH 173950, 173951, 173969, 173971, 173976, 173978, 174125, 174127, 174131–174135, 174139, 174140, 174143, 174148, 174150, 174155, 174158, 174199, 174201, 186581–186584, 186586. **Charlottesville:** AMNH 259938, 259940, 259943, 259945–259949, 259951–259967.

TABLE 14

Hato El Frio: MHNLS 7906–7908, 7910–7912, 7915–7918, 7920–7922, 7924–7926, 7931, 7934–

7936, 7938, 7940, 7941, 7943; USNM 448678–448685, 448687–448695, 448697–448701, 448704, 448705. **Parcela 200:** MHNLS 3782–3784, 3787–3802, 3804, 3805, 3807, 3808, 3839, 3840, 3842–3844, 3846. **Río Chico:** USNM 388003, 388013, 388021, 388023, 388025–388027, 388038, 388040, 388042, 388044, 388047, 388049–388052, 388054, 388056, 388058, 388059, 388061, 388081, 388083, 388084, 388089, 388090, 388093–388096, 388098, 388099, 388101. **San Antonio Maturín:** AMNH 69800, 69802, 69804–69821. **Finca Vuelta Larga:** AMNH 257316, 257318–257320, 257322, 257324–257332, 257356; MHNLS 8133, 8134, 8137, 8144, 8145, 8147–8150, 8153–8156, 8160, 8161.

TABLE 15

Villavicencio: AMNH 136346, 136349, 142180–142183, 142186, 142187, 142189, 142190, 142193–142196; MVZ 106227; ROM 75226; USNM 507281–507286, 507288. **San Juan Manapiare:** USNM 409992, 409996, 409997–410000, 416723–416725, 416732, 416734, 416739, 416743, 416745–416747, 416749–416751, 416753, 416754. **Belén:** USNM 406174–406176, 406178, 406181–406183, 406186–406188, 406198–406200, 406202–406206, 406209, 406212. **Esmeralda:** AMNH 77088, 77089, 77091, 77253, 77254, 77256–77258, 77315–77317; MBUCV 1478, 1479, 1678, 1679, 1682, 1683, 1727, 1728, 1731, 1732, 1736, 1737, 1739, 1743, 1770, 1771, 1800.

TABLE 16

Auyántepeui: AMNH 130839, 130841, 130847–130849, 130851–130856, 130858, 130860, 130864, 130865, 131022, 131023, 131130, 131133, 131137, 131139, 131140, 131145. **San Ignacio Yuruani:** AMNH 257308, 257310, 257313, 257314; MHNLS 7842, 7847, 7853–7856, 7872, 7897, 8051–8053, 8055, 8068; USNM 448641–448647, 448649. **Roraima:** AMNH 75544, 75545, 75711, 75714–75717, 75719, 75720, 75724, 75725, 75738, 75742, 75746, 75749, 75750, 75752, 75754, 75755, 75844. **Limão:** AMNH 75354, 75355, 75357, 75359, 75365–75368, 75371, 75374–75377, 75380–75383, 75385, 75386, 75390, 75391, 75464, 75486, 75487, 75491–75494, 75496, 75500, 75501, 75504, 75505, 75507, 75509, 75510, 75512.

TABLE 18

Isla Cébaco: USNM 360261–360271, 360273–360287, 360290–360294, 360296–360307, 360309, 360360, 360436, 360437, 360440–360444. **San Miguel Island:** AMNH 25991–25995; FMNH 18482, 18483, 18486, 18487; MCZ 8481, 8482, 8484, 8492, 8493, 8495, 8498, 8500, 9073, 9075, 9076, 12563, 12564, 12566, 12567, 12569, 12570, 12572, 12574, 12576, 12578, 12592, 12593, 12595, 12596; UMMZ 104327, 104344; USNM 116670–116672.

TABLE 19

Finca Helechales: USNM 547957, 547959–547961, 547963, 547965, 547966, 547969–547974, 547977–547979, 547981, 547982, 547985, 547988. **Montijo Bay:** UMMZ 104285, 104286, 104288, 104289, 104294, 104296, 104297, 104299, 104306, 104309, 104310–104314, 104317, 104319, 104320, 104321, 104323, 104329–104340, 104342. **Cerro Azul:** USNM 302494, 302507, 302509, 302513–302517, 302519–302522, 302524, 302686, 302687, 302690, 302693–302695, 303107–303112, 303114, 303115, 303117, 303118, 303121–303123, 303125, 303126, 303245, 303256, 303257, 303297.

TABLE 20

Villanueva: USNM 280454, 280463, 280465–280467, 280470, 280471, 280474, 280479, 280482, 280485, 280487–280490, 280496, 280498, 280499, 280502, 280507, 280508, 280510, 280512–280514, 280516, 280518, 280522, 280523. **Misión Tukuko:** MHNLS 7699, 7701, 7702, 7709, 7710, 7715, 7716, 7718, 7719, 7721, 7725–7727, 7729, 7757, 7758, 7766, 7799, 7815; USNM 448657, 448659, 448660, 448664–448677. **Hacienda Socopito:** USNM 442381–442384, 442387, 442388, 442390, 442391, 442393, 442394, 442397, 442399, 442402–442405, 442407, 442409, 442410–442413. **Urama:** USNM 372527–372533, 372535–372537, 374617, 374632, 374633, 374637, 374638, 374640–374642, 374644, 374645, 374647, 374650–374655, 374659, 387985, 387987.

TABLE 21

Paramaribo: BMNH 52.1145; RMNH 21588–21590, 21597, 21606, 21607, 21617 (A, B, E, F, H, N, O, P, Q, Z), 21628, 21950, 21952–21957, 22382, 22385. **Cayenne:** MNHN 76-361, 76-362, 76-364, 76-365, 86-904, 86-906 to 86-913, 86-919, 86-931 to 86-935, 86-951. **Cacao:** MNHN 80-242 to 80-249, 80-251 to 80-256, 86-547, 86-548, 86-631, 86-632, 86-637 to 86-640, 86-1064.

APPENDIX 2

Specimens Dissected for Gall Bladders

AKODONTINI

Akodon (Abrothrix) longipilis (MVZ 163725, 163726).
Akodon (Akodon) azarae (UMMZ 134440, 137562).
A. (A.) boliviensis (AMNH 262692, 262722).
A. (A.) cursor (AMNH 248412, 248413, 248419–248422; UMMZ 124285–124288).
A. (A.) dayi (UMMZ 156245, 156306).
A. (A.) toba (UMMZ 125502, 125605).
A. (A.) urichi (AMNH 259908, 259910–259913).
A. (Chroeomys) jelskii (AMNH 81278, 81284, 81285, 241615, 241616).
Bolomys lasiurus (AMNH 211826, 211833, 211837, 211851, 211860, 211898, 214520, 214521, 214529, 214531, 214534, 214535).
Chelemys macronyx (MVZ 171177, 175809).
Geoxus valdivianus (MVZ 155844, 163735).
Lenoxus apicalis (MVZ 171511, 171516, 171517, 172346).
Microxus bogotensis (UMMZ 155607–155618).

M. mimus (AMNH 261193, 261195–261202, 261204).
Oxymycter delator (AMNH 248518; UMMZ 124290, 124295, 124297, 124298).
Podoxomys roraimae (AMNH 75582–75586).

ICHTHYOMYINI

Anotomys leander (AMNH 244606, 244607; UMMZ 126295, 126296, 155599, 155600, 155601).
Chibchanomys trichotis (MBUCV 2796; UMMZ 156376, 156532).
Ichthyomys hydrobates (AMNH 64624, 244610; UMMZ 156375).
I. pittieri (MBUCV I-2776, I-2803).
I. tweedii (UMMZ 126300, 155782–155788).
Neusticomys monticolus (UMMZ 126299, 155789, 155790, 155793, 155794).
N. venezuelae (AMNH 69907, 69908, 257344, 257345).

Rheomys mexicanus (AMNH 182139, 185018, 205313, 205320).

R. raptor (UMMZ 111985–111987, 116934).

R. thomasi (MVZ 98802, 98806).

R. underwoodi (UMMZ 115389, 115459, 115460, 116935).

ORYZOMYINI (oryzomyine group)

Microryzomys altissimus (AMNH 248277, 248279, 248280, 248497).

M. minutus (AMNH 248278).

Neacomys tenuipes (AMNH 257269–257271).

Nectomys squamipes (AMNH 235058, 235069; UMMZ 124189, 124191, 124193).

Nesoryzomys narboroughi (MVZ 145383, 145385).

Oecomys bicolor (AMNH 257268).

O. flavicans (AMNH 257267).

O. speciosus (USNM 448583).

O. trinitatis (AMNH 259998, 256000).

Oligoryzomys chacoensis (AMNH 247758, 247759, 247766, 247769, 247770).

O. delticola (AMNH 235422, 235424–235426, 235968, 235970).

O. flavescens (AMNH 206010).

O. fulvescens (AMNH 257245, 257246, 257248, 257250–257252).

O. microtis (AMNH 263326–263328, 263334, 263335, 263340, 263369).

Oryzomys (*Macruroryzomys*) *hammondi* (UMMZ 155827).

O. (Melanomys) caliginosus (UMMZ 111961, 111962, 111965).

O. (Oryzomys) albigularis (UMMZ 155805, 155806).

O. (O.) alfaroi (UMMZ 155811, 155814).

O. (O.) capito (UMMZ 125230–125234).

O. (O.) macconnelli (USNM 448584, 448585).

O. (O.) palustris (AMNH 239256, 239258–239261, 239263, 239264).

O. (O.) ratticeps (AMNH 248407–248411).

O. (O.) talamancae (AMNH 257239).

O. (O.) xantheolus (UMMZ 155915–155917).

Scolomys melanops (USNM 399936).

Sigmodontomys alfari (USNM 499972, 499974, 499975).

ORYZOMYINI (thomasomyine group)

Aepeomys lugens (MBUCV I-2793, I-2794).

Chilomys instans (AMNH 63370–63372; UMMZ 155619, 155620).

Delomys dorsalis (BMNH 14.2.23.13, 84.2.8.37, 84.2.8.38, 86.9.16.3, 86.9.16.4).

Rhipidomys couesi (AMNH 263135, 263154).

R. fulviventer (UMMZ 156377, 156378, 156379).

R. leucodactylus (AMNH 241643).

R. macconnelli (AMNH 75587–75593, 75598, 75603, 75849).

R. mastacalis (AMNH 257273–257275; USNM 448612, 448615, 448624, 448626, 448628).

Thomasomys aureus (AMNH 248281, 248498; UMMZ 155624–155626).

T. baeops (UMMZ 155627–155632).

T. daphne (UMMZ 156195, 156196).

T. hylophilus (USNM 495624, 495626, 495627).

T. laniger (UMMZ 156380, 156381).

T. paramorum (AMNH 248282; UMMZ 155656, 155657, 155659, 155664).

T. rhoadsi (UMMZ 155752, 155753).

T. sylvestris (UMMZ 155762, 155763, 155766).

PHYLLOTINI

Andalgalomys pearsoni (UMMZ 130037, 134386).

Andinomys edax (AMNH 249021, 249023).

Auliscomys pictus (AMNH 232649, 232650; UMMZ 160541).

Calomys callosus (AMNH 246923–246928).

Chinchillula sahamae (AMNH 247885, 247886).

Eligmodontia typus (MVZ 158413, 163737).

Euneomys petersoni (MVZ 172200).

Graomys domorum (UMMZ 155872, 155874).

G. griseoflavus (AMNH 248438, 248440, 248441–248444).

Irenomys tarsalis (MSU 7466, 7468, 7470).

Neotomys ebriosus (AMNH 232645–232647, 241678).

Phyllotis amicus (UMMZ 158035, 158036).

P. andium (UMMZ 155918).

P. darwini (UMMZ 155852, 155853).

P. osilae (AMNH 81280, 241400, 241401, 241403, 241405).

Reithrodon physodes (AMNH 206361).

SCAPTEROMYINI

Kunsia tomentosus (BMNH 79.325–79.327).

Scapteromys tumidus (AMNH 235453, 235491, 235492, 235502).

SIGMODONTINI

Sigmodon alstoni (AMNH 257337–257340).

S. hispidus (USNM 526192, 526197, 526205, 526227, 526234).

Holochilus brasiliensis (AMNH 257335, 257336).

H. magnus (AMNH 206373, 206388).

SIGMODONTINAE INCERTAE SEDIS

Pseudoryzomys simplex (one specimen dissected for tissues in the field by P. Myers).

Zygodontomys brevicauda (AMNH 75848, 75855, 142257, 202645, 255818, 255819, 259950–259962; UMMZ 111957, 111959, 111960).

APPENDIX 3

Specimens of *Sylvilagus floridanus* Examined

Below are listed the specimens of *Sylvilagus floridanus* that document the pattern of geographic variation in nape color illustrated in figure 40. Specimens without definite geographic information or bearing unidentifiable place-names are not listed. *Italic type* identifies Venezuelan state names.

NETHERLANDS ANTILLES: Aruba (AMNH 149382, FMNH 16611), Curaçao (AMNH 32663, FMNH 16578). VENEZUELA: *Anzoátegui*, Cantaura (one uncataloged specimen in MHNLS), 14 km W Clarinas (USNM 406714–406717, 406719, 406721, 406725–406729, 406731), Mamo (MHNLS 5801); *Apure*, Hato Cariben (USNM 374274–374279), Mantecal (MHNLS 3766–3768); *Aragua*, Maracay (FMNH 16579, one uncataloged specimen in MHNLS); *Bolívar*, Ciudad Bolívar (MHNLS 933); *Carabobo*, Montalbán (USNM 441984); *Cojedes*, Apartadero (MHNLS 556), Carretera Tinaco-El Baúl km 80 (MHNLS 4720, 4721), La Sierra (MHNLS 5), 38 km SE Las Vegas (MHNLS 3880, 3881, 4112–4115); *Falcón*, Capatárida (USNM 441994), Carretera Cabure-San Luis (MHNLS 615–617, 2437, 3449), Carretera Coro-Churuguara km 40 (MHNLS 3882), Jun-

calito (USNM 441998), Moruy (AMNH 132866; USNM 456556, 456284, 456285, 456288–456294, 456296–456298, 456300, 456302–456305); *Guárico*, 16 km NW Barbacoas (USNM 374269, 374270), Calabozo (MHNLS 525), 40 km N Calabozo (MHNLS 1647, 2599), El Sombrero (AMNH 143006), Las Mercedes (MHNLS 3384–3389, 3648), Sta. Maria Ipire (MHNLS 384), Zaraza (AMNH 135470); *Lara*, El Tocuyo (AMNH 32067–32070), Río Tocuyo (AMNH 130601–130603, 130605, 130606), San Miguel (AMNH 132774); *Monagas*, Hato Mata de Bejuco (USNM 441987–441993); *Nueva Esparta*, Isla Margarita (FMNH 16616, MHNLS 182–188, USNM 405944, 405946–405949); *Sucre*, 2 mi W Guamache (three uncataloged specimens in MHNLS); *Yaracuy*, Salom (MHNLS 827), Yaritagua (MHNLS 1899, 1900, 1925–1927, 2230, 2231, 2424, 2425, 3521); *Zulia*, Maracaibo (FMNH 18697, 18699, 18700, 20536, 22074), Río Cogollo (FMNH 22075, 22076), Río Yasa (MHNLS 872, 873), Villa del Rosario (MHNLS 7997, 7998), Machiques (MHNLS 95), Hda. La Frontera (MHNLS 4383).

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