



Taxonomy, Distribution, and Natural History of the Genus *Heteromys* (Rodentia: Heteromyidae) in Western Venezuela, with the Description of a Dwarf Species from the Península de Paraguaná

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Source: American Museum Novitates, 2003(3396) : 1-43

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2003\)396<0001:TDANHO>2.0.CO;2](https://doi.org/10.1206/0003-0082(2003)396<0001:TDANHO>2.0.CO;2)

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AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3396, 43 pp., 12 figures, 4 tables March 27, 2003

Taxonomy, Distribution, and Natural History of the Genus *Heteromys* (Rodentia: Heteromyidae) in Western Venezuela, with the Description of a Dwarf Species from the Península de Paraguaná

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ABSTRACT

Heteromys anomalus is widely distributed along the Caribbean coast of South America and was generally considered the only spiny pocket mouse present in Venezuela until *H. australis* was reported recently from the Cordillera de Mérida. Here, I revise the spiny pocket mice of western Venezuela and compare specimens from the semi-insular Península de Paraguaná with samples from throughout the distributional area of *H. anomalus*. Morphological comparisons with all other species of the genus suggest that the *Heteromys* from Paraguaná are closely related to *H. anomalus*, but univariate and multivariate analyses show that they are much smaller than samples of *H. anomalus*. In addition, adults from Paraguaná display differences in cranial shape when compared with adults of *H. anomalus*. Hence, specimens from Paraguaná are here described as a new species, *Heteromys oasicus*, and taxonomic treatments of *H. anomalus* and *H. australis* in western Venezuela are also provided. Although the original geographic context of this case of dwarfism in body size is unknown, *H. oasicus* currently appears to be isolated in mesic vegetation on the low Cerro Santa Ana and Fila de Monte Cano, which lie in a matrix of tropical thorn forest. The new species represents one of the few vertebrates considered endemic to Paraguaná, but basic inventories and taxonomic studies are not yet complete in the region.

RESUMEN

Heteromys anomalus está ampliamente distribuido a lo largo de la costa caribeña de Suramérica y había sido considerada la única especie de ratón de abazones (= ratón mochilero; ratón bolsero; ratón bolsón) presente en Venezuela, hasta que *H. australis* fue reportado recientemente para la Cordillera de Mérida. En el presente estudio se revisa la taxonomía de los *Heteromys* del occidente de Venezuela y se comparan ejemplares de la Península de Paraguaná con muestras representativas de toda la distribución geográfica de *H. anomalus*. Las comparaciones morfológicas con las restantes especies del género indican que los ratones mochileros de Paraguaná están estrechamente relacionados con *H. anomalus*, pero los análisis univariados y multivariados demuestran que aquéllos poseen un tamaño corporal mucho menor que las series analizadas de *H. anomalus*. Además, las proporciones craneanas en los adultos de Paraguaná muestran diferencias con respecto a los adultos de *H. anomalus*. Por lo tanto, se describen a los ejemplares de Paraguaná como representantes de una especie nueva, *Heteromys oasicus*. Además, se presentan resúmenes taxonómicos para *H. anomalus* y *H. australis* en el occidente de Venezuela. Aunque no se conoce definitivamente el contexto geográfico original de este caso de enanismo de tamaño corporal, actualmente *H. oasicus* parece confinada a vegetación relativamente húmeda en el Cerro Santa Ana y la Fila de Monte Cano, que se encuentran rodeados por una matriz de espinares y matorrales secos tropicales. La nueva especie representa a una de los pocos vertebrados que se consideran endémicos de Paraguaná; no obstante, el inventario básico de la región aún no ha sido realizado de manera exhaustiva y resulta indispensable el desarrollo de estudios taxonómicos detallados para la mayoría de los taxones.

INTRODUCTION

Spiny pocket mice (*Heteromys* and *Liomys*) belong to the family Heteromyidae, which originated in North America (Wood, 1935; Hershkovitz, 1969, 1972; Rogers, 1990; Webb, 1997). These two genera form the subfamily Heteromyinae, a monophyletic group within the family (Hafner, 1981; Hafner and Hafner, 1983; Wahlert, 1985). The center of extant heteromyid diversity lies in the southwestern United States and Mexico,

and *Heteromys* is the only genus of the family to have colonized South America, where it is restricted to the northwestern portion of the continent.

Spiny pocket mice are terrestrial granivores found primarily in forested habitats (Sánchez-Cordero and Fleming, 1993). Species of *Liomys* inhabit deciduous forests and other semiarid tropical habitats from southern Texas to Panama (Genoways, 1973; Williams et al., 1993). In contrast, species of *Heteromys* inhabit wetter (usually evergreen)

forests from southern Mexico to northwestern South America. Although a few morphological characters exist to diagnose the genera (Williams et al., 1993), their reciprocal monophyly has not yet been demonstrated in any phylogenetic analysis (see Rogers [1990] for poorly resolved phenetic clustering of species based on variation at allozyme loci). Six (Williams et al., 1993) or seven (Patton, 1993) species of *Heteromys* have been recognized in recent faunal lists, but current taxonomy underestimates the true diversity of the genus (Rogers, 1990; Patton, 1993; Anderson, 1999). Recently, Anderson and Jarrín-V. (2002) described an additional species from Ecuador.

Two species of *Heteromys* are known to be widespread in South America, and two have restricted distributions. *Heteromys anomalus* inhabits both deciduous and evergreen tropical forests in northern South America, typically up to ca. 1500–1600 m. It is distributed along the Caribbean coast of Colombia and Venezuela (including Isla Margarita) and in Trinidad and Tobago (Musso-Q., 1962; Handley, 1976; Anderson, 1999; Anderson and Soriano, 1999), but not in Panama (Anderson, 1999; contra Rogers, 1990; Méndez, 1993; Williams et al., 1993; Nowak, 1999). The species is also known from parts of the dry Magdalena Valley in Colombia (Hernández-Camacho, 1956; Anderson, 1999). In contrast, *H. australis* is restricted to very mesic evergreen forests in the Chocó of northwestern Ecuador, western Colombia, and eastern Panama, as well as throughout much of the Colombian Andes up to ca. 2500 m in elevation (Anderson, 1999). A disjunct population also exists in the Uribante drainage of the Cordillera de Mérida in western Venezuela (Anderson and Soriano, 1999; Anderson et al., 2002). In addition to these widespread taxa, a new species (*H. teleus*) was recently described from central-western Ecuador, where it inhabits evergreen but highly seasonal forests (Anderson and Jarrín-V., 2002). Finally, a species of the *Heteromys desmarestianus* complex (provisionally referred to as *H. d. crassirostris*) is present in high montane regions of the Serranía del Darién in extreme northwestern Colombia (Anderson, 1999), west of the Río

Atrato/Río San Juan lowlands (= Bolívar Geosyncline; Hershkovitz, 1972).

Before *Heteromys australis* was reported for Venezuela (Anderson and Soriano, 1999), most recent publications listed *H. anomalus* as the only pocket mouse present in the country (e.g., Eisenberg, 1989; Soriano and Ochoa-G., 1997; Linares, 1998). Previously, however, Handley (1976) had noted the presence of an undescribed species of *Heteromys* from the Península de Paraguaná in northwestern Venezuela (see fig. 1). This arid peninsula is connected to the rest of the mainland only by a “long, narrow sparsely vegetated isthmus” (Handley, 1976: 78; see also Barnes and Phelps, 1940; Romero, 1989; Markezich and Taphorn, 1994; Markezich et al., 1997). The *Heteromys* from Paraguaná were found solely from the base and upper slopes of a low, isolated mountain (Cerro Santa Ana), which lies in a xeric lowland matrix of thorn forest characteristic of most of the peninsula. In contrast, the upper slopes of Cerro Santa Ana hold cloud forest and other mesic vegetation above approximately 550 m, a low proportion of its surface (Bisbal-E., 1990). Further specimens were reported from Cerro Santa Ana as *H. anomalus* by Bisbal-E. (1990), who captured them only on the upper slopes of the *cerro*. Additionally, two heretofore unreported specimens exist from the Fila de Monte Cano (see appendix 1), a nearby low ridge that is predominantly covered by thorn forests but that also includes relatively mesic vegetation along a seasonal watercourse (Romero, 1989; M. Díaz, in litt.).

In the present study, I evaluate the taxonomic status of populations of *Heteromys* from the Península de Paraguaná. To do so, I complete the revision of *H. anomalus* in Colombia (begun in Anderson, 1999), extend it to western Venezuela, and make quantitative comparisons with large series and type material available from Colombia, Venezuela, and Trinidad. Future work will revise the genus in eastern Venezuela.

MATERIALS AND METHODS

MUSEUM SPECIMENS

Eight hundred twenty-four specimens from the following museum collections form

the basis of this report (abbreviations follow Hafner et al., 1997; Lew and Ochoa, 1993; and Bisbal-E. and Sánchez-H., 1997; an asterisk denotes collections with material from western Venezuela, as defined below):

AMNH	American Museum of Natural History, New York*
ANSP	Academy of Natural Sciences, Philadelphia
CM	Carnegie Museum of Natural History, Pittsburgh*
CVULA	Colección de Vertebrados de la Universidad de los Andes, Mérida*
EBRG	Museo de la Estación Biológica de Rancho Grande, Maracay, Aragua*
FMNH	Field Museum [formerly Field Museum of Natural History], Chicago*
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá
IND-M	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (= IAvH; includes former INDERENA collection), Villa de Leiva, Boyacá
KU	University of Kansas Natural History Museum, Lawrence*
LACM	Natural History Museum of Los Angeles County, Los Angeles
MBUCV	Museo de Biología de la Universidad Central de Venezuela, Caracas*
MCNUSB	Museo de Ciencias Naturales de la Universidad Simón Bolívar, Baruta/Caracas*
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MHNSL	Museo de Historia Natural La Salle, Caracas*
MLS	Museo del Instituto La Salle, Bogotá
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
UF	Florida Museum of Natural History, University of Florida, Gainesville*
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum of Natural History, Washington, DC*
UV	Universidad del Valle, Cali
UWZM	University of Wisconsin Zoological Museum, Madison*

I examined specimens for discrete characters and patterns of variation in the external and cranial anatomy. Cranial nomenclature follows Wahlert (1985), Anderson (1999), and Anderson and Jarrín-V. (2002). Based on patterns of toothwear and molt,

specimens were assigned to the age classes of Rogers and Schmidly (1982). Age classes 1–3 represent juveniles and subadults, whereas classes 4–6 are progressively older adults. Age classes do not constitute a continuous variable (such as absolute age), but rather are categories roughly corresponding to relative age within population samples (see Voss et al., 1990).

Material reported here from the principal study area (appendix 1) includes the overwhelming majority of specimens of *Heteromys* from western Venezuela available in museums in the United States and Venezuela (and all that I have examined). Note, however, a few important records from the Venezuelan *llanos* (tropical savannas) reported by Utrera et al. (2000), which I have not examined. Western Venezuela is here considered as the area west of the Depresión de Yaracuy (SAGCN, 1995; ≈ Depresión de Lara sensu Soriano et al., 1999). This lowland region separates the Cordillera de Mérida from the Cordillera de la Costa (fig. 1) and, for the purposes of this paper, is delimited by the rivers Yaracuy, Cojedes, and Apure (not shown). In addition, I report all specimens of *H. anomalus* known to me from Colombia, including some not noted in Anderson (1999). For statistical analyses, I take advantage of the several largest series of that species available from localities throughout its range (see Geographic Variation). Finally, I compare these *Heteromys* qualitatively with representative samples of all other currently accepted species of the genus, including the majority of extant holotypes (appendix 2). Where original elevation was reported in feet, I provide that datum as well as the metric equivalent to the nearest whole number.

MEASUREMENTS

Standard cranial measurements for *Heteromys* (fig. 2) follow Anderson and Jarrín-V. (2002). I took these measurements to the nearest 0.01 mm with digital calipers (except for specimens from the ICN collection, which were measured to the nearest 0.1 mm with dial calipers) on intact skulls from selected localities as described below and listed in appendix 3. External measurements and

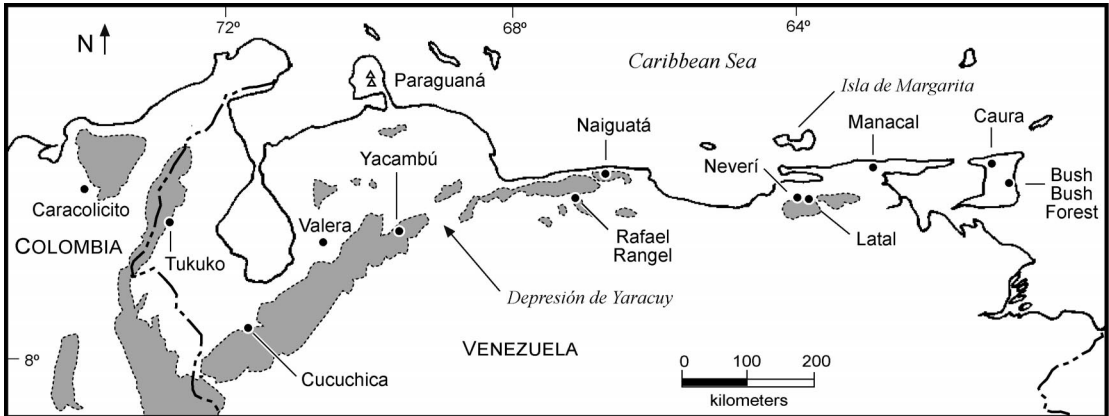


Fig. 1. Map of north-central South America showing the approximate position of primary geographic samples of *Heteromys anomalus* (●) and of *Heteromys* from the Península de Paraguaná (△) used here. Gray shading approximates regions more than 1000 m in elevation. See appendices 1 and 2 for complete provenience and museum catalog numbers and appendix 3 for a list of measured specimens.

mass were copied from specimen tags and, when necessary, from primary field notes.

Occipitonasal length (ONL): greatest distance from anteriormost projection of nasal bones to posteriormost portion of occipital bone.

Zygomatic breadth (ZB): greatest width across zygomatic arches at right angle to longitudinal axis of cranium.

Rostral length (RL): greatest distance from notch lateral to lacrimal bone to anteriormost projection of nasal bone on same side of cranium.

Nasal length (NL): greatest distance from anteriormost projection of one nasal bone to its posteriormost projection (not necessarily at medial suture between nasals).

Least interorbital constriction (IOC): least width across interorbital constriction at right angle to longitudinal axis of cranium.

Squamosal breadth (SB): width across squamosal anterior to external auditory meatus at right angle to longitudinal axis of cranium.

Maxillary tooththrow length (MTR): distance from anterior lip of alveolus of premolar to posterior lip of alveolus of third molar.

Interparietal width (IW): greatest transverse width measured from lateralmost projections of interparietal bone at right angle to longitudinal axis of cranium.

Interparietal length (IL): greatest distance from anteriormost projection of interparietal bone to posteriormost border of interparietal bone, always taken along medial line of cranium even when notch present in posterior border.

Parietal breadth (PB): greatest width across pa-

rietal crests at right angle to longitudinal axis of cranium.

Skull depth (SD): greatest distance from dorsal-most point of braincase to horizontal plane passing through ventral borders of maxillary cheek teeth and ventral borders of occipital condyles (taken by placing skull on glass microscope slide with upper incisors rested over edge of slide, and then subtracting thickness of slide).

STATISTICAL ANALYSES

GENERAL PROTOCOLS: Except where otherwise noted, statistical analyses were performed with Minitab (1996; version 11.12). Probability levels reported here should be regarded as approximate, given moderate sample sizes in most groups that preclude tests of multivariate normality. These approximate probabilities were compared to a significance level of $\alpha = 0.05$ for all tests, except where modified to adjust for multiple tests (see below). Descriptive statistics were calculated for specimens from the Península de Paraguaná and for the 12 primary geographic samples of *H. anomalus* (see Geographic Variation) in age class 4, which was the most abundant adult age class.

Principal components analyses (PCA) were conducted on the covariance matrix of log-transformed measurements following Jolicoeur (1963); natural logarithms (\log_e or

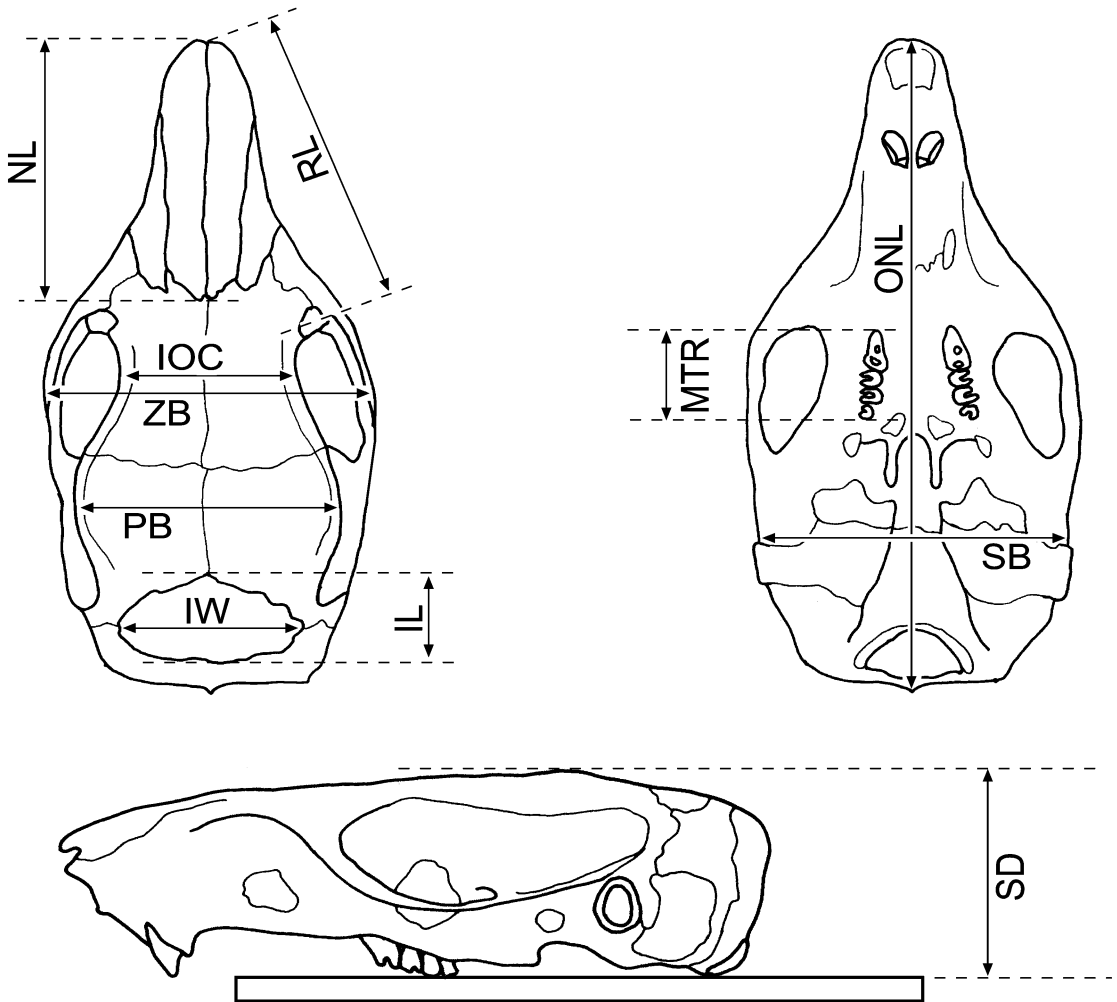


Fig. 2. Dorsal, ventral, and lateral views of a cranium of *Heteromys*, showing method of taking cranial measurements. Abbreviations and measurements are defined in the Materials and Methods.

ln) were used here. PCA is a multivariate ordination technique that extracts axes of maximum dispersion among specimens without regard to the group (e.g., geographic sample) to which specimens belong. Each resultant axis (principal component) is characterized by an eigenvector with coefficients that indicate the relationship of each variable to that multivariate axis. I also present principal components as loadings, which are Pearson product-moment correlation coefficients between specimen scores on each axis and the \log_e -transformed variables. Both unit eigenvectors and loadings are commonly used to identify and explain multivariate axes, yield-

ing similar interpretations. I only interpreted principal components with clearly distinct eigenvalues (by inspection). For visual presentation of specimen scores on multivariate axes, I scale the axes of a given analysis relative to their eigenvalues (proportion of variation explained) in plots of specimen scores on those axes.

Discriminant function (DFA) and canonical variates (CVA) analyses were performed in SAS 6.12 for UNIX (SAS, 1990; PROC DISCRIM and PROC CANDISC) on \log_e -transformed cranial measurements. A DFA tests for differences among centroids (multivariate means) of groups (e.g., geographic

samples) specified by the investigator. Significance for comparisons between particular pairs of geographic samples in the DFAs was determined using F -statistics of Mahalanobis distances between pairs of group centroids and Holm's (1979) modification of the Bonferroni procedure correcting for multiple comparisons. Here, statistical power varies for each pair according to the sample sizes involved. Complementary to DFA, CVA is an ordination technique that extracts multivariate axes that maximize variation among group centroids. For interpretation, I present these canonical axes solely as loadings. I explain and further discuss only canonical axes with clearly distinct eigenvalues.

GEOGRAPHIC VARIATION: I quantitatively compared adult specimens of *Heteromys* from the Península de Paraguaná with 12 geographic samples of *Heteromys anomalus* from Colombia, Venezuela, and Trinidad (all in age class 4; fig. 1). The sample from Paraguaná included specimens from both Cerro Santa Ana and Monte Cano (*Paraguaná*, Estado Falcón). The samples of *H. anomalus* included one in northern Colombia (*Caracolicito*, Departamento del Cesar), nine across northern Venezuela (*Tukuko*, Estado Zulia; *Cucuchica*, Estado Mérida; *Valera*, Estado Trujillo; *Yacambú*, Estado Lara; *Rafael Rangel*, Estado Aragua; *Naiguatá*, Estado Vargas; *Neverí*, Estado Sucre; *Latal*, Estado Sucre; and *Manacal*, Estado Sucre), and two in Trinidad and Tobago (*Caura*, Trinidad, and *Bush Bush Forest*, Trinidad). These geographic samples were chosen for their relatively large sample sizes and geographic dispersion. In some cases, nearby localities were pooled to create the samples (appendices 1 and 3).

To examine the multivariate structure of the data and determine how much of the variation among specimens of the same age class corresponds to geographic variation, specimens in age class 4 from these samples were submitted to a principal components analysis with males and females pooled. A one-way analysis of variance (ANOVA) was performed by geographic sample on $PC1_{geo}$ scores, testing for differences in means among samples on that axis. Tukey's comparisons between all pairs of sample means on $PC1_{geo}$ were also conducted to determine

which particular pairs of geographic samples were significantly different from each other. The statistical power for each pair varied according to the sample sizes involved.

Additionally, to test for differences in multivariate means among geographic samples and to examine the basis of any differences present, a DFA and CVA were conducted on the same dataset with geographic sample denoting group membership. An ANOVA with Tukey's comparisons was performed for scores on $C1_{geo}$, as for $PC1_{geo}$ from the PCA. I also conducted a second DFA/CVA with the putative species forming the only two groups: the Paraguaná specimens versus all other samples pooled together.

COMPARISONS AMONG TYPE SAMPLES: A second PCA was conducted comparing the sample from Paraguaná with material representing *Heteromys anomalus* and the other nominal taxa considered synonyms of it. Adults of age classes 4–6 were analyzed together here to take maximal advantage of small sample sizes. A one-way ANOVA and Tukey's comparisons by nominal taxon were conducted on specimen scores on the resulting $PC1_{type}$. When possible, I used measurements from holotypes and associated type series that I have examined: *H. anomalus hershkovitzi* Hernández-Camacho, 1956; *H. jesupi* Allen, 1899; and *H. anomalus brachialis* Osgood, 1912. To represent the nominotypical form described from "Trinidad" (Thompson, 1815), I used early collected specimens from Caura (on the island of Trinidad) as well as measurements for the holotype of *H. anomalus* reported by Williams et al. (1993). Thus, this PCA was conducted only using RL, NL, IOC, and MTR (the four measurements available for the holotype of *H. anomalus*). I did not have access to the holotypes of *H. melanoleucus* Gray, 1868 or *Perognathus bicolor* (Gray, 1868), both of which Williams et al. (1993) considered full synonyms of *H. a. anomalus*. Apparently, no holotype exists for *H. thompsonii*, a name that Lesson (1827) clearly used to refer to the spiny pocket mouse from Trinidad named by Thompson (1815).

In addition to the holotype of *Heteromys jesupi*, Allen (1899) mentioned 12 other examined specimens from various localities in the same region (all in the vicinity of Santa

Marta, Colombia) in his description of that taxon. In total, 13 specimens of *Heteromys* (AMNH 15344–15356) were cataloged in sequence along with the type, but they do not correspond exactly to the localities listed by Allen. I suggest that his first mention of Bonda (Allen, 1899: 201) should read Onaca, and that he included two specimens from El Líbano Plantation in the count for the nearby locality Masinga Vieja. Thus, I use these 13 specimens to represent the type series of *H. jesupi*.

SYSTEMATICS

The analyses indicate the presence of three species of *Heteromys* in western Venezuela, for which I provide the following taxonomic treatments. Except for the one record of *H. australis* known from the country (Anderson and Soriano, 1999), all specimens examined from western Venezuela outside the Península de Paraguaná match the characterization of *H. anomalus* presented in Anderson (1999). Clear differences separate the Paraguaná *Heteromys* from all other species of the genus except *H. anomalus*, which is quite similar to it in discrete morphological characters. However, the species of spiny pocket mouse present on the Península de Paraguaná differs from *H. anomalus* by strikingly smaller body size, cranial proportions of adults, and pelage characters. To refer to it, I propose the name:

***Heteromys oasicus*, new species**
Paraguaná Spiny Pocket Mouse

Figures 3, 7

HOLOTYPE: USNM 456325; adult male; skin and skull in excellent condition (fig. 3). Collected on 25 July 1968 by Norman E. Peterson from Venezuela: Estado Falcón: 49 km N, 32 km W of Coro, Cerro Santa Ana, at 550 m. Original number SVP (Smithsonian Venezuelan Project) 24036.

PARATYPES: The following specimens (adults skins and skulls in good condition) from the type locality are designated as paratypes: EBRG 15110, 15111; USNM 456327.

ETYMOLOGY: Latinized from the Greek *oasis* (a fertile spot in a desert) using the Latin suffix *-icus*, belonging to or pertaining to (Brown, 1956), in reference to the species'



Fig. 3. Dorsal, ventral, and lateral views of the holotype of *Heteromys oasicus* (USNM 456325), a male in age class 4.

restricted distribution along watercourses and other relatively mesic areas on Cerro Santa Ana and Monte Cano. There, suitable habitat for the species exists due to mist coming off the ocean, surrounded by a matrix of xerophytic habitat on the remainder of the Península de Paraguaná.

DISTRIBUTION: Known only from Cerro Santa Ana (fig. 4) and the Fila de Monte Cano on the Península de Paraguaná, Estado Falcón, Venezuela. Likely restricted to small areas of evergreen and semideciduous vegetation on the peninsula (figs. 5, 6).

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters: p4 (lower permanent premolar) with 3 lophs; P4 (permanent upper premolar) with straight, moderately deep fold in anterior border of posterior loph; mesopterygoid fossa V-shaped, with long, thin hamular processes of pterygoids; optic foramen small, with exterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest



Fig. 4. Landscape at Cerro Santa Ana (localities 101 and 102; Estado Falcón), showing vertical stratification of vegetation types on its slopes. **Upper:** View of Cerro Santa Ana from the WNW. Note

posterior to its widest point, then ascending dorsally to rejoin crest near its posterior termination; braincase absolutely narrow and only weakly ridged; interorbit strongly constricted; rostrum short and strongly tapered (in dorsal view); skull relatively diminutive (ONL 29.7–31.6 mm in examined adult specimens) and gracile; body size extremely small for genus, with hind foot 30 mm or less in adults; dorsal pelage always harsh and spiny, very pale brown and strongly grizzled with thin ochraceous hairs intermixed among spines; no lateral ochraceous band present on flanks; little or no dark coloration on forelimbs; plantar surface of hind feet naked.

DESCRIPTION: Dorsal pelage spiny and extremely pale for genus, but still contrasting with soft, pure-white pelage of venter; pelage thin (both spines and other hairs), especially behind ears and on flanks; ears pale brown and large relative to body size (appendix 4); tail strongly bicolored, slightly longer than head-and-body length; forearms white, with little or no brown hairs present; hind feet small, with naked plantar surface; skull small (appendix 4) and gracile; anterior half of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; anterior roots of zygomatic arches gracile; interorbital constriction very narrow; braincase absolutely narrow and flat, not inflated; parietal and temporal crests weak; interparietal moderately wide and rounded laterally, sometimes with slight anterior point; incisive foramina long and fairly thin, slightly tapering anteriorly; no swelling at anterodorsal border of infraorbital foramen; mesopterygoid fossa V-shaped, with long, thin hamular processes of pterygoids; postalar fissure large and distinctly rounded anteriorly; optic foramen small, with exterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point, then ascending dorsally to rejoin crest near its posterior termination; dental formula: (inci-

sors 1/1, canines 0/0, premolars 1/1; molars $3/3 \times 2 =$ total 20; molars small, with lophes of upper M2 subequal in width; lateral borders of lophes of molars smooth, not pointed; P4 with straight, moderately deep fold in anterior border of posterior loph, and with smoothly curved posterior border; p4 with 3 lophes; m3 not reduced, approximately same width as p4; angular process of mandible flat and blunt.

MEASUREMENTS OF THE HOLOTYPE (MM): Total length 227, tail length 120, hind foot length 29, ear length 18, ONL 31.18, ZB 14.72, RL 13.18, NL 12.11, IOC 7.45, SB 13.94, MTR 4.93, IW 7.81, IL 4.49, PB 11.81, and SD 9.93. Mass 50.5 g.

COMPARISONS: *Heteromys oasicus* is externally similar to species of *Liomys*, which are also small and pale; because generic limits between *Heteromys* and *Liomys* have not been corroborated by genetic analyses (Rogers, 1990) or any modern phylogenetic treatment, explicit character comparisons with *Liomys* are merited. *Heteromys oasicus* differs from species of *Liomys* by the following characters: V-shaped mesopterygoid fossa, with long, thin hamular processes of pterygoids; p4 with 3 lophes; moderately deep fold in anterior margin of posterior loph of P4; smooth (rather than laterally pointed) lophes on molars; and small optic foramen, with exterior margin formed by strong bar of bone (see also Genoways, 1973; Williams et al., 1993).

The extremely pale, grizzled pelage of the new species clearly separates it externally from all other species of *Heteromys* except *H. gaumeri* and *H. anomalus* (which is typically pale—see account of that species). In contrast to *H. oasicus*, specimens of *H. gaumeri* (from the Yucatán peninsula of Mexico, Belize and Guatemala) have haired plantar surfaces of the hind feet. The pale dorsal pelage of *H. oasicus* contrasts especially sharply with the dark, slaty gray pelage of both *H. australis* (which is widespread in northwest-

←

evergreen cloud forest above ca. 550 m (darker areas near the summit), where *Heteromys oasicus* was most commonly collected. Deciduous forest is present on lower slopes of the *cerro*, and thorn forest covers the surrounding lowlands. **Lower:** View of Cerro Santa Ana from the NNW. Note tongues of evergreen forest descending down streambeds. Photographed by José Ochoa-G. in May 2002.

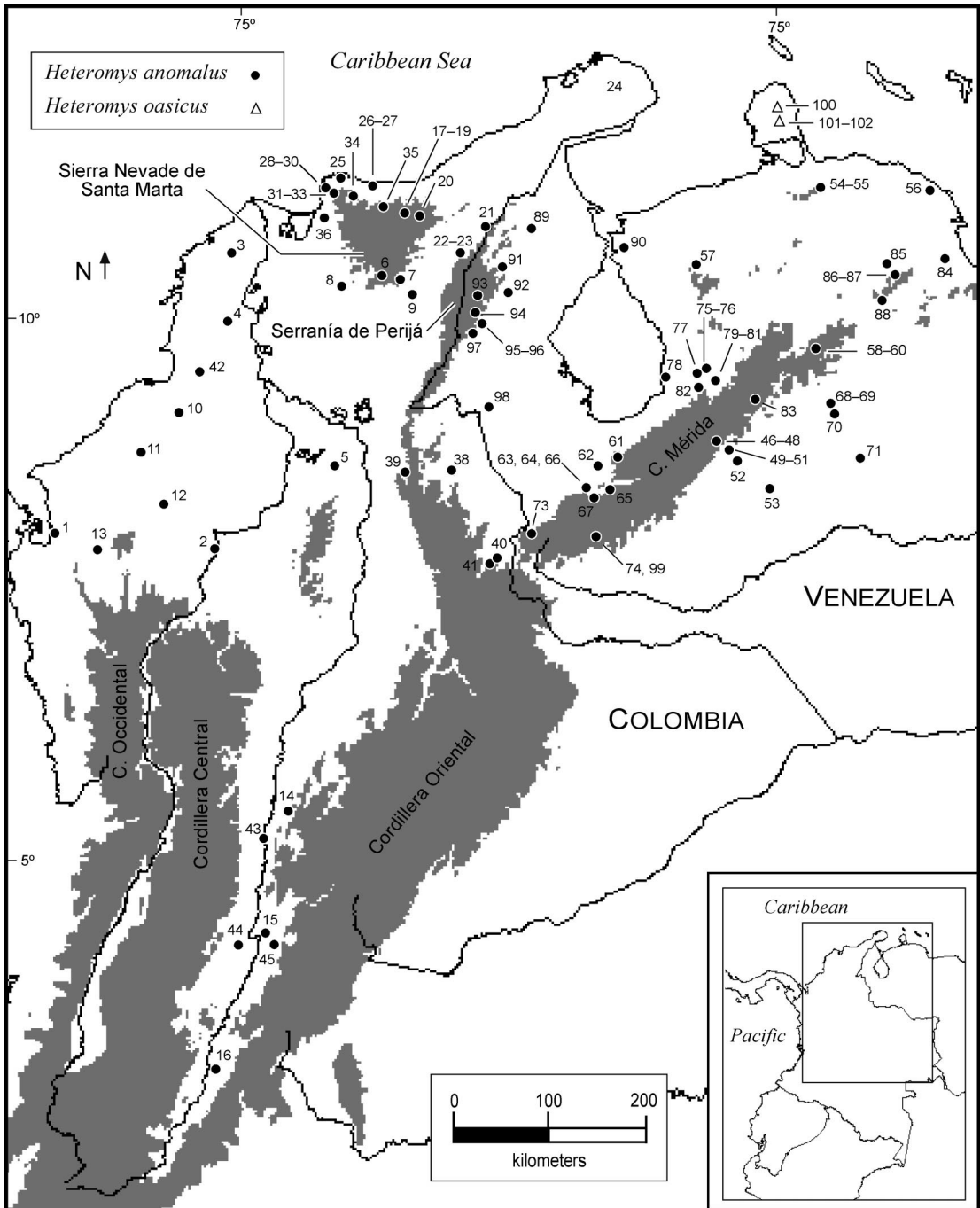


Fig. 5. Map of northwestern South America showing collection localities of *Heteromys oasicus* (Δ) and *Heteromys anomalus* (\bullet) in Colombia and western Venezuela. Localities are numbered to correspond with information given in the Gazetteer (appendix 1). *Heteromys anomalus* continues its distribution to the east in north-central and northeastern Venezuela, but *H. oasicus* is endemic to the Península de Paraguaná. One locality of *H. australis* is known from Venezuela (locality 99, overprinted here by locality 74 of *H. anomalus*), but that species is primarily distributed to the west in Panama, Colombia,

ern South America and known from one locality in the Cordillera de Mérida in western Venezuela) and *H. teleus* (from western Ecuador). Furthermore, some species of the genus (i.e., *H. gaumeri* and many populations of the *H. desmarestianus* complex) have a distinctive lateral ochraceous stripe on the flanks, lacking in *H. oasicus*.

Cranially, *Heteromys oasicus* is dwarfed by most species of the genus, especially by *H. oresterus*, *H. nelsoni*, and most species of the *H. desmarestianus* complex (following Williams et al. [1993] in considering *H. goldmani* a synonym of *H. desmarestianus*). In addition, the short, wide rostrum of *H. oasicus* distinguishes it from the long, thin rostrum of *H. oresterus* (from the Cordillera de Talamanca, Costa Rica) and the long, massive one of *H. nelsoni* (present in southern Mexico and western Guatemala). *Heteromys teleus* is much larger and more robust than *H. oasicus* and has especially wide zygomatic arches. *Heteromys oasicus* has an absolutely narrow, flat braincase in sharp contrast to the wide, inflated one of *H. australis*. No species of the *H. desmarestianus* complex matches the combination of small size, narrow braincase, and short rostrum found in *H. oasicus*. The new species differs from *H. gaumeri* by the narrow postalar fissure and strongly concave anterior termination of the premaxillary (creating a step in the lateral border of the rostrum) of this last taxon.

Heteromys oasicus is most similar to *H. anomalus*, with which closer comparisons are required. The sister-species status between the two is tentatively supported by (pending full phylogenetic analysis of the subfamily and formal character polarization): placement of parietomastoid suture, which dips well ventral to parietal crest posterior to its widest point and then ascends dorsally to rejoin crest near its posterior termination; a

narrow, elongated braincase; and large ears relative to body size. Along with *H. australis* and *H. teleus* (other South American species), these two species also show a straight, moderately deep fold in the anterior border of the posterior loph of P4 and an especially small optic foramen. Furthermore, both *H. oasicus* and *H. anomalus* typically have pale, strongly grizzled pelage (present in all specimens of *H. oasicus* and most populations of *H. anomalus*), but this character state—while uncommon in *Heteromys*—is probably plesiomorphic within the subfamily (Anderson, unpubl.).

Despite these similarities, adult body size is markedly smaller in *Heteromys oasicus* than in *H. anomalus* (appendix 4, figs. 7–9). The PCA of geographic variation revealed no overlap in overall size ($PC1_{geo}$; fig. 8, table 1) between adults of age class 4 of the two species, even with very broad geographic sampling of *H. anomalus* (including insular populations from Trinidad). Scores on $PC1_{geo}$ were significantly different among geographic samples ($P < 0.001$), primarily reflecting the extremely small body size of specimens from Paraguaná (*H. oasicus*) and the moderately small size of individuals of *H. anomalus* from Bush Bush Forest, on the island of Trinidad (table 2). Similarly, mean scores on the first canonical axis ($C1_{geo}$, also a size axis; fig. 9, table 3) were different among geographic samples ($P < 0.001$), with samples from Paraguaná and from Bush Bush Forest different from all other groups and from each other (table 2). When *Heteromys oasicus* was compared directly with all samples of *H. anomalus* pooled together, the centroids for the two species were distinct ($P < 0.0001$). The canonical axis separating them ($C1_{geo}$) was a measure of size (with large specimens having positive scores; table 3), and no overlap existed between the two species on it.

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and Ecuador (see maps of Anderson, 1999; Anderson and Soriano, 1999; Anderson et al., 2002; Anderson and Jarrín-V., 2002). Only georeferenced localities are plotted here with symbols. Three localities (24, 37, and 72) could not be precisely located; because it is specifically mentioned in the text, the approximate position of locality 24 (Serranía de La Macuira) is indicated on the map without a symbol. Gray shading indicates regions more than 1000 m in elevation. See appendix 1 for complete provenience and museum catalog numbers.

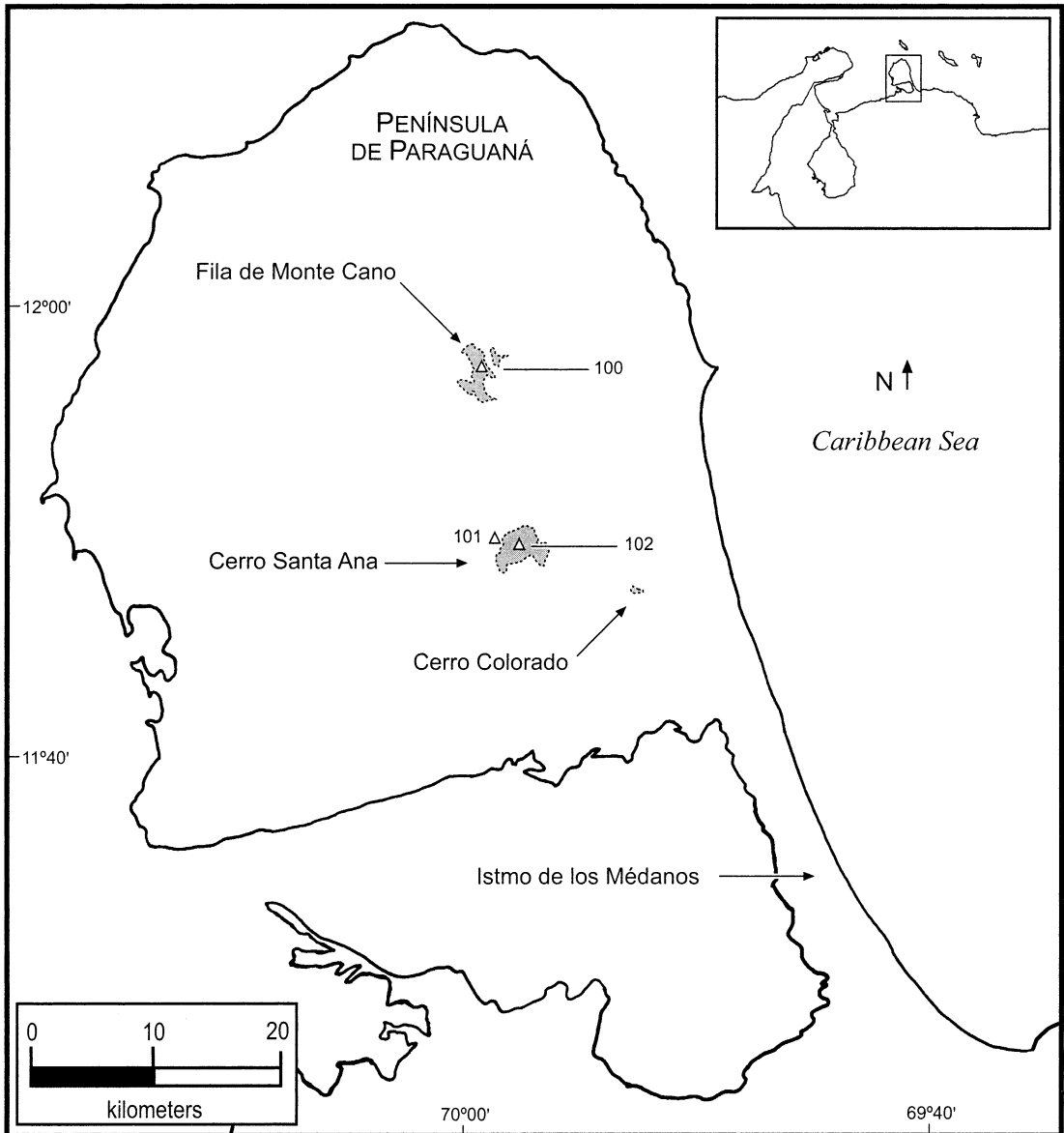


Fig. 6. Map of the Península de Paraguaná showing the location of major geographic features and collection localities of *Heteromys oasicus* (Δ ; see appendix 1 for complete provenience and museum catalog numbers). Gray shading indicates regions above 200 m; the small area above ca. 550 m on Cerro Santa Ana that supports evergreen cloud forest is largely overprinted by the symbol for locality 102.

Similarly, the descriptive statistics show that *Heteromys oasicus* has consistently smaller averages than does *H. anomalus* for all cranial measurements (appendix 4). In fact, for univariate measurements of adults in age class 4, values for tail length and hind

foot length in all specimens of *H. oasicus* are smaller than those for any examined Venezuelan individuals of *H. anomalus*, but the observed range for *H. oasicus* on those measurements overlaps with that of the insular population of *H. anomalus* from Bush Bush

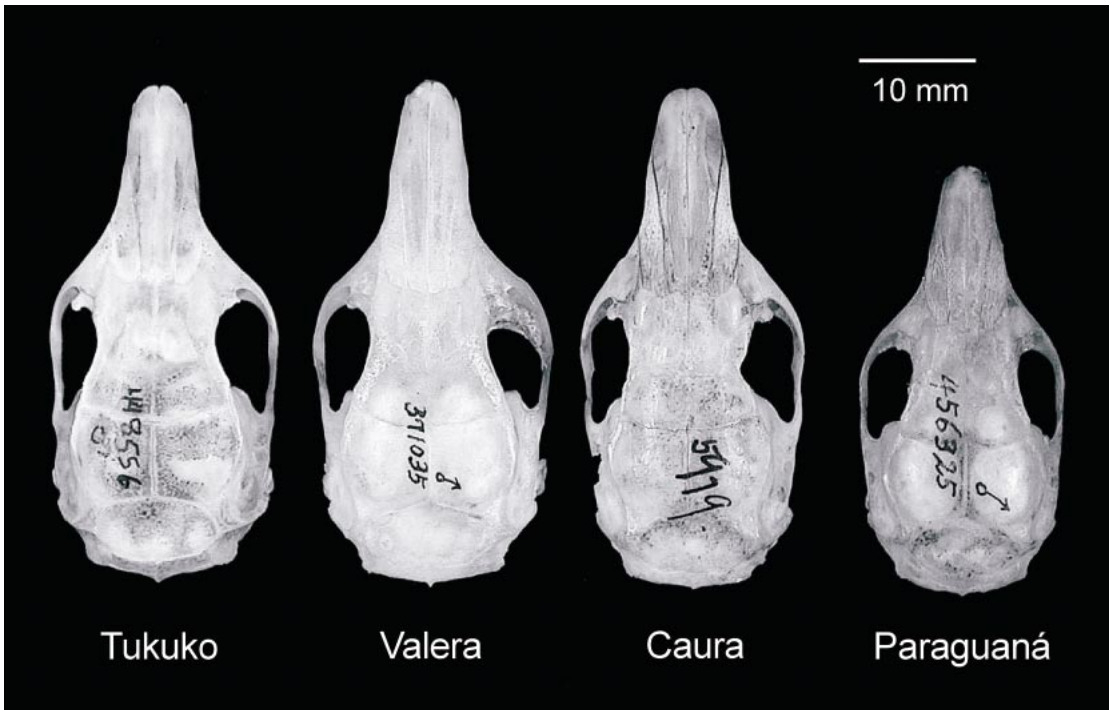


Fig. 7. Dorsal views of skulls of *Heteromys anomalus* from Tukuko (Zulia, Venezuela), Valera (Trujillo, Venezuela), and Caura (Trinidad) and of *H. oasicus* from the Península de Paraguaná (Falcón, Venezuela). All specimens are males in age class 4.

Forest (Trinidad). However, no overlap was observed in rostral length between adults in age class 4 of the two species. Furthermore, a plot of rostral length for age series of the Paraguaná populations and Latal—the largest ontogenetic series of *H. anomalus* available from the South American mainland—confirms the extreme shift in development between the two species (fig. 10). Rostral length was chosen to represent body size because it correlates highly with growth in this group (Anderson, unpubl.) and was available for most specimens of *H. oasicus*. In these samples, even adults of *H. oasicus* in age class 5 are smaller than specimens of *H. anomalus* in age class 2. Although specimens of *H. anomalus* from Bush Bush Forest were smaller on average than other samples of that species for most measurements (see also results of multivariate analyses, above), the observed ranges for Bush Bush Forest overlap those of the mainland samples. The moderate difference in mean for various measures of body size between the insular population of

H. anomalus at Bush Bush Forest and others of that species is negligible when compared with the extremely small size of *H. oasicus* (showing no overlap with specimens of *H. anomalus*).

Heteromys oasicus is also morphometrically distinct from the type series of *Heteromys anomalus* and its examined synonyms (fig. 11). The first principal component of this analysis represented a size factor (with large specimens having negative scores; table 4). Locality means differed on $PC1_{type}$ ($P < 0.001$), with *H. oasicus* different from the other four series (the only other significant pairwise comparison being between *H. a. brachialis* and *H. a. hershkovitzi*). The holotype of *H. anomalus* showed the lowest score on $PC1_{type}$, identifying it as the largest specimen overall.

In addition to these striking differences in body size, adults of *Heteromys oasicus* and *H. anomalus* differ in cranial shape (figs. 3, 7) and external coloration. On average, *Heteromys oasicus* has relatively shorter,

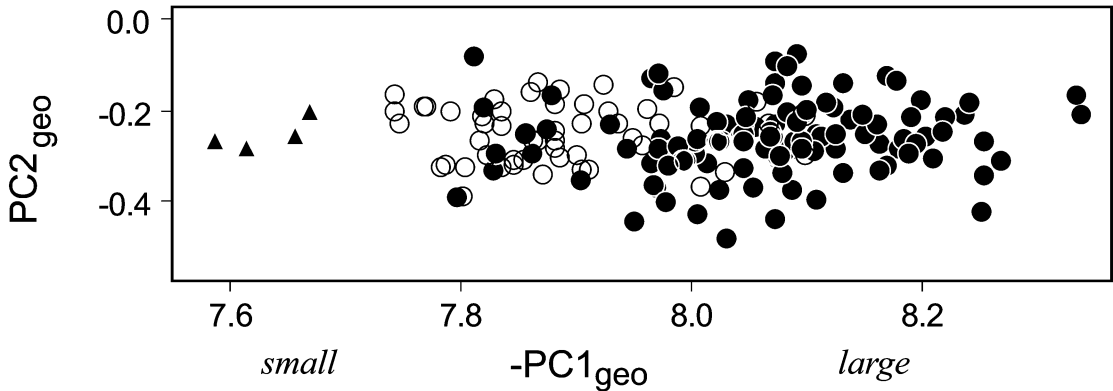


Fig. 8. Plot of specimen scores on the first two axes of the principal components analysis (PCA) of geographic variation performed on 174 specimens of *Heteromys* in age class 4 without regard to geographic sample. $PC1_{geo}$ represents a size factor and was here multiplied by -1 so that smaller specimens appear to the left and larger ones to the right (table 1). Axes are scaled relative to their eigenvalues (proportion of variation among specimens explained). Specimens of *H. oasiscus* are marked by solid triangles, and individuals of *H. anomalous* are denoted by circles (solid circles for the South American mainland and open circles for the island of Trinidad). Note the strikingly small size of specimens of *H. oasiscus*.

more strongly tapering nasals and a relatively wider (but still absolutely narrower) braincase than *H. anomalous* (by inspection). In addition, the temporal fossa is shallow, the in-

terorbital region flat, and the anterior root of the zygomatic arch gracile. While the incisive foramina of *H. anomalous* are variable geographically, those of *H. oasiscus* are char-

TABLE 1

Results of Principal Components Analysis (PCA) of Geographic Variation Conducted on 174 Specimens of *Heteromys oasiscus* and *H. anomalous* in Age Class 4 (see fig. 8)

Elements of the unit eigenvector (*left*) and loadings (*right*) are presented for the first three principal components. Cranial measurements were transformed to their natural logarithms before components were extracted from the covariance matrix. Eigenvalues (multiplied by 100) and the percent of variation among specimens explained are given for each axis.

	Unit eigenvectors			Loadings		
	$PC1_{geo}$	$PC2_{geo}$	$PC3_{geo}$	$PC1_{geo}$	$PC2_{geo}$	$PC3_{geo}$
ln-ONL	-0.324	-0.130	0.129	-0.926	-0.193	0.178
ln-ZB	-0.303	-0.112	0.035	-0.898	-0.173	0.049
ln-RL	-0.375	-0.233	0.197	-0.890	-0.286	0.224
ln-NL	-0.411	-0.245	0.199	-0.892	-0.276	0.208
ln-IOC	-0.313	-0.112	0.004	-0.827	-0.153	0.005
ln-SB	-0.241	0.021	-0.061	-0.833	0.037	-0.101
ln-MTR	-0.268	-0.090	0.061	-0.726	-0.127	0.080
ln-IW	-0.340	0.312	-0.808	-0.622	0.296	-0.710
ln-IL	-0.243	0.854	0.454	-0.443	0.804	0.396
ln-PB	-0.199	0.080	-0.187	-0.718	0.149	-0.324
ln-SD	-0.228	-0.050	-0.044	-0.819	-0.092	-0.076
Eigenvalue ($\times 100$)	2.029	0.545	0.467			
% variation explained	57.3%	15.4%	13.2%			

TABLE 2
 Approximate Statistics for Morphometric Separation Among Geographic Samples of *Heteromys oasicus* (Paraguana) and *H. anomalus* (remaining 12 samples)

F-statistics with 11 and 151 degrees of freedom are given for Mahalanobis distances between pairs of group centroids, with significant comparisons appearing in **bold**. Below the F-statistic, pairs are marked by PCI (principal component 1) and/or CI (canonical axis 1) if their mean scores on those respective axes were significantly different by Tukey's tests of multiple comparisons with familywide error rates of $\alpha = 0.05$. Probabilities attached to all tests should be regarded as approximate due to moderate sample sizes in most samples.

	Paraguana	Caracolcito	Tukuko	Cucuchica	Valera	Yacambú	Rafael Rangel	Naiguatá	Neverí	Latal	Manacal	Caura
Caracolcito	11.84 PCI, CI											
Tukuko	10.23 PCI, CI	7.99										
Cucuchica	7.40 PCI, CI	5.05	1.64									
Valera	7.70 PCI, CI	6.34	4.37	1.47								
Yacambú	9.67 PCI, CI	9.22 CI	5.66 PCI	2.81	3.53							
Rafael Rangel	11.20 PCI, CI	8.96	4.01	2.14	2.82	5.30 CI						
Naiguatá	8.84 PCI, CI	8.99	5.39 PCI	2.05	5.66	7.82	3.47 PCI					
Neverí	12.24 PCI, CI	8.77	5.68	2.89	3.75	5.20 PCI	4.00	6.53 PCI				
Latal	13.38 PCI, CI	6.20	6.34	3.47	5.34	6.28 CI	4.59	4.20	2.80			
Manacal	6.38 PCI, CI	7.78 CI	5.41 CI	2.61 CI	2.97	6.08	5.41 CI	4.80 CI	2.42 CI	4.60 CI		
Caura	6.35 PCI, CI	5.46 CI	2.40	2.00	3.27	1.81	4.15 CI	2.51	1.81	2.28 CI	1.39	
Bush Forest	4.43 PCI, CI	15.47 PCI, CI	15.47 PCI, CI	6.99 PCI, CI	7.63 PCI, CI	12.72 PCI, CI	12.48 PCI, CI	14.19 PCI, CI	9.87 PCI, CI	14.73 PCI, CI	3.52 PCI, CI	2.97 PCI, CI

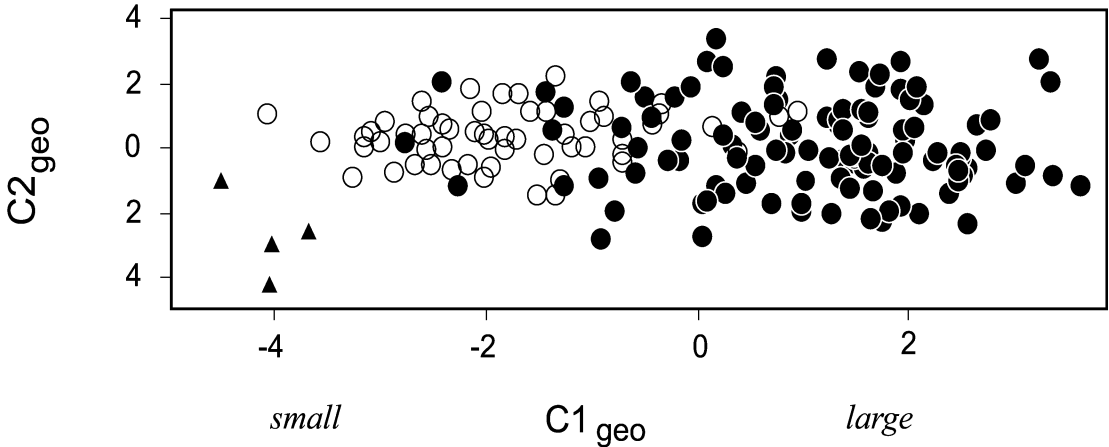


Fig. 9. Plot of specimen scores on the first two axes of the canonical variates analysis (CVA) of geographic variation performed on specimens of *Heteromys* in age class 4 from the 13 geographic samples. Axes are scaled relative to their eigenvalues (proportion of variation among centroids of geographic samples explained). Specimens of *H. oasicus* are marked by solid triangles, and individuals of *H. anomalus* are denoted by circles (solid circles for the South American mainland and open circles for the island of Trinidad). The first canonical axis can be interpreted as a measure of size (table 3), with large specimens having positive scores.

TABLE 3

Results of Canonical Variates Analyses (CVAs) of Geographic Variation Conducted on Specimens of *Heteromys oasicus* and *H. anomalus* in Age Class 4 (see fig. 9)

Loadings are presented for the first three canonical axes of the CVA performed with 13 geographic samples (*left*) and for the only canonical axis of the CVA for *H. oasicus* versus the 12 pooled samples of *H. anomalus* (*right*). Cranial measurements were transformed to their natural logarithms before axes were extracted that maximally separate the group centroids. Eigenvalues and the percent of variation among group centroids explained are given for each axis.

	13 localities			<i>H. oasicus</i> vs. <i>H. anomalus</i>
	C1 _{geo}	C2 _{geo}	C3 _{geo}	C1 _{species}
ln-ONL	0.791	0.362	-0.053	0.792
ln-ZB	0.671	0.227	-0.219	0.717
ln-RL	0.789	0.443	0.004	0.873
ln-NL	0.769	0.311	0.180	0.768
ln-IOC	0.750	0.068	-0.167	0.643
ln-SB	0.799	-0.018	-0.286	0.610
ln-MTR	0.589	0.407	-0.237	0.800
ln-IW	0.710	-0.387	-0.033	0.267
ln-IL	0.169	0.444	-0.048	0.447
ln-PB	0.793	-0.001	-0.059	0.526
ln-SD	0.773	0.135	-0.375	0.720
Eigenvalue	2.878	0.807	0.763	0.301
% variation explained	47.0%	13.2%	12.5%	100%

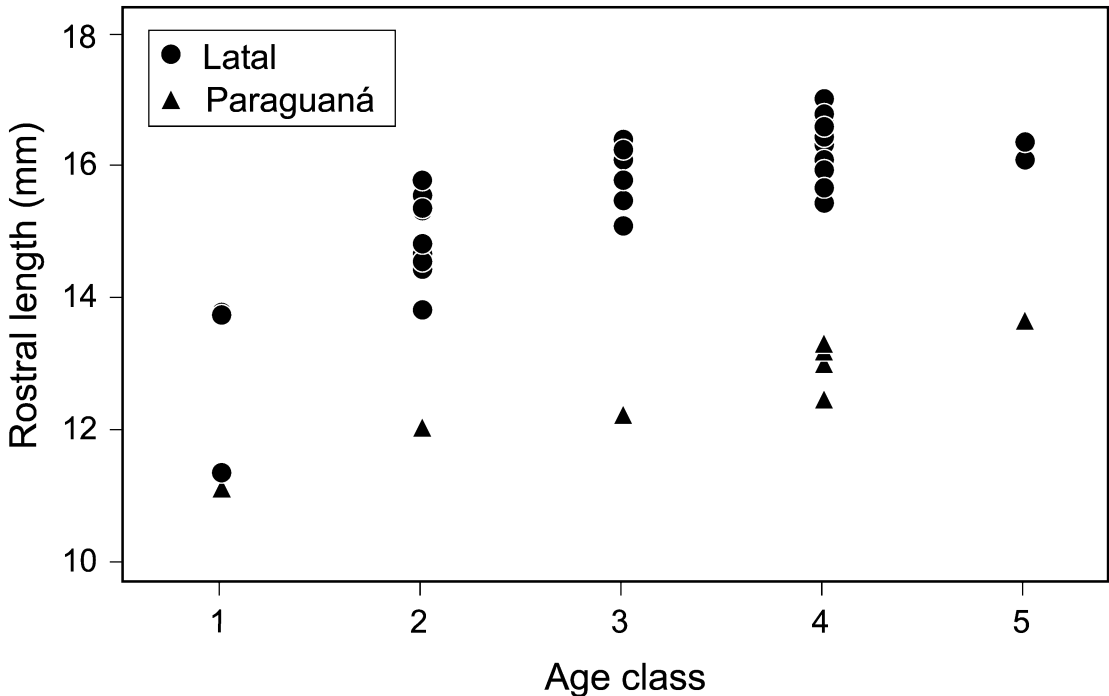


Fig. 10. Plot of rostral length (RL) versus age class for specimens of *Heteromys oasicus* from the Península de Paraguaná, Venezuela (▲) and of *H. anomalus* from Latal, Venezuela (●). Rostral length was chosen to represent overall size here, because it correlated highly with growth in the group (Anderson, unpubl.) and was available for most specimens from Paraguaná. Age classes do not represent a continuous variable (such as age in days), but rather categories roughly corresponding to relative age (see text and Voss et al., 1990). Note the extremely small size of specimens of *H. oasicus*, with the adult in age class 5 smaller than individuals of age class 2 in the Latal sample of *H. anomalus*.

acteristically long and thin. Externally, the species are very similar, but the dorsum of *H. oasicus* is even paler than any examined population of *H. anomalus*. Furthermore, most specimens of the new species lack any dark coloration on their forearms, with other individuals having only a faint wash of dark hairs there. Conversely, *H. anomalus* has a distinct patch of dark color (typically connected to the dark coloration of the flanks) on its forelimbs, as is typical for the genus.

COMMENTS: Handley (1976) tentatively assigned a specimen from Estado Guárico: Hato Los Leones, Caño Agua Frío, 23 km NE of Calabozo, 89 m (USNM 387822; the only *Heteromys* specimen in the SVP collection from the llanos) to the species of *Heteromys* from the Península de Paraguaná (referred to as *Heteromys* sp. A). He noted that it was a juvenile with tiny feet, and that the dusky color of forearm and flanks was dis-

continuous. My examinations indicate that USNM 387822 represents an extremely young individual of *H. anomalus*. It is a male in age class 1, very young even for that age class—representing the smallest body size trappable in *H. anomalus*. This specimen matches another juvenal *H. anomalus* (USNM 409812 from Estado Sucre: 8 km N, 5 km E of Güiría, Hacienda La Concordia, 7 m) in age, size, mass, and cranial proportions. Although USNM 387822 from Hato Los Leones does have the dusky color of the flanks and forearms discontinuous (as noted by Handley, 1976), that is also true of many individuals of *H. anomalus*. Detailed comparisons reveal that it is the absence or extreme reduction of the dusky patch on the forearm that is characteristic of *H. oasicus*.

NATURAL HISTORY: In contrast to several studies reporting a variety of data for populations ascribed to *Heteromys anomalus* (Pir-

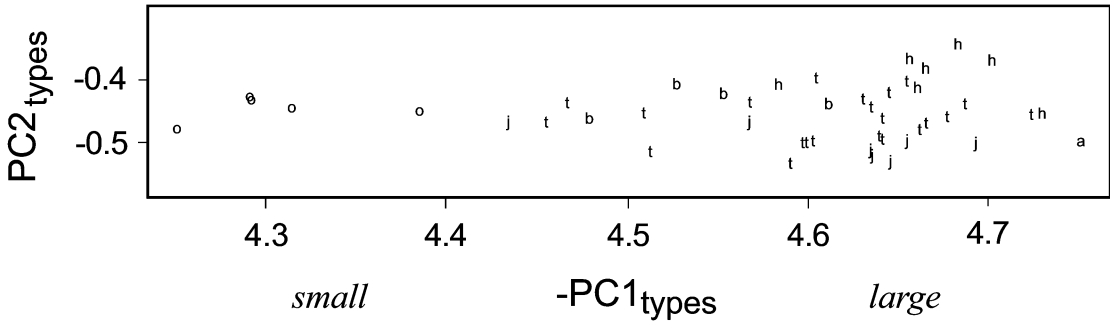


Fig. 11. Plot of specimen scores on the first two axes of the principal components analysis (PCA) of type series of *Heteromys oasicus* and *H. anomalous* and its synonyms. Adults in age classes 4–6 were used here. $PC1_{type}$ represents a size factor and was multiplied by -1 so that smaller specimens appear to the left and larger ones to the right (table 4). Axes are scaled relative to their eigenvalues (proportion of variation among specimens explained), and specimens are marked by the first letter of the following respective series: a, *anomalous*; b, *brachialis*; h, *hershkovitzi*; j, *jesupi*; o, *oasicus*; t, Trinidad (Caura, used as an additional sample of the nominotypical *anomalous*). Note the small size of specimens of *H. oasicus*, especially in contrast to the holotype of *H. anomalous*.

lot, 1963; Rood, 1963; Rood and Test, 1968; August, 1984; Valdez et al., 1985; Soriano and Clulow, 1988), only scarce ecological information is available for *H. oasicus* from Cerro Santa Ana and the Fila de Monte Cano. The physiographic and climatological conditions that create mesic environments conducive to the species' presence evidently vary on the two formations, according to their elevation. Cerro Santa Ana (fig. 4) shows a distinct vertical zonation of habitats from its base to the peak at 850 m (Bisbal-E., 1990). Xerophytic thorn forest occurs up

to 300 m. From there, deciduous montane forest extends to 550 m, where it is replaced by evergreen cloud forest. Finally, dwarf mesic vegetation occupies the remaining 150 m of the *cerro*. The base of Cerro Santa Ana (at ca. 170 m) receives an average annual precipitation of 458 mm in a unimodal regime (wet season from September to January; dry season the remainder of the year). Areas above 550 m are mesic with well-developed humid soils, due to condensation of water coming off the ocean and, secondarily, by the presence of several springs

TABLE 4

Results of Principal Components Analysis (PCA) of Type Series of *Heteromys oasicus* and *Heteromys anomalous* and Its Synonyms (see fig. 11)

Adults in age classes 4–6 were used here. Elements of the unit eigenvector (*left*) and loadings (*right*) are presented for the first three principal components. Cranial measurements were transformed to their natural logarithms before components were extracted from the covariance matrix. Eigenvalues (multiplied by 100) and the percent of variation among specimens explained are given for each axis.

	Unit eigenvectors			Loadings		
	$PC1_{type}$	$PC2_{type}$	$PC3_{type}$	$PC1_{type}$	$PC2_{type}$	$PC3_{type}$
ln-RL	-0.619	0.514	0.066	-0.941	0.288	0.037
ln-NL	-0.586	0.141	0.229	-0.957	0.085	0.136
ln-IOC	-0.296	-0.729	0.560	-0.656	-0.595	0.451
ln-MTR	-0.430	-0.430	-0.794	-0.794	-0.293	-0.533
Eigenvalue ($\times 100$)	1.481	0.202	0.196			
% variation explained	76.6%	10.4%	10.1%			

above 700 m (Bisbal-E., 1990; see also Barnes and Phelps, 1940).

In contrast, the Fila de Monte Cano is much lower and drier, with a completely different relief (Romero, 1989, including photograph; Markezich and Taphorn, 1994). It is better described as a ridge rather than a hill, peak, or mountain. Miriam Díaz (in litt.) provided the following characterization (translation mine): "Monte Cano has a maximum elevation of 250 m, with high temperatures of 30°C, low temperatures of 21°C, and relative humidity between 60 and 90%. The most common vegetative formations belong to dry and very dry tropical forest, with denser formations in the gallery forests or streambeds. Due to its proximity to the sea, mist accumulates in the morning hours, although it has no permanent rivers or streams."

Most specimens of *Heteromys oasicus* derive from cloud forest and mesic stunted vegetation types above 550 m on Cerro Santa Ana (Handley, 1976; Bisbal-E., 1990). The lone specimen known from thorn forest near the base of Cerro Santa Ana (Handley, 1976) was collected near an intermittent stream holding "standing pools of water with a great deal of moss" (N. Peterson field notes and collection card, July 1968). This individual is a juvenal male in age class 1; future trapping is necessary to determine whether adults also inhabit such habitats along the slopes of the *cerro*.

Angela Martino-G. kindly provided unpublished information regarding the only known specimens of *Heteromys oasicus* from Monte Cano. All were captured among terrestrial bromeliads in the bed of a seasonal stream, which was dry at the time. This small stream, which is the only significant watercourse in the Monte Cano reserve, flows through deciduous forest; however, trees along the stream form a semideciduous formation that maintains shade throughout the year (A. Martino-G., in litt.). Even this semideciduous riparian forest is quite short, not exceeding 10 m in height (J. Ochoa-G., personal commun.). Traps were also placed in the reserve outside the streambed, but they yielded no *Heteromys*. I have examined two specimens from Monte Cano; one is an adult female, and the other a juvenal male. Four

additional specimens (one male and three females) were collected at the same time and were recently cataloged at the Museo de Historia Natural La Salle (MHNLS 11148–11151; A. Martino-G. and D. Lew, in litt.), but I have not examined them.

Given what is known about the species, these two populations are probably isolated from each other by arid thorn forest, which extends throughout the lowlands of the peninsula (Markezich et al., 1997). In addition to the two known populations of *Heteromys oasicus*, the only other plausible area that the species could inhabit is Cerro Colorado, a hill ca. 7 km ESE of Cerro Santa Ana that reaches just over 200 m in elevation (fig. 6; Markezich et al., 1997, for photograph). Cerro Colorado is not known for the complicated mosaics of xeric and mesic vegetation present on Cerro Santa Ana and Monte Cano, however (Romero, 1989; Bisbal-E., 1990; Markezich and Taphorn, 1994; Markezich et al., 1997); thus, presence of the species there is unlikely. The known populations of *H. oasicus* are surely disjunct from the distribution of *H. anomalus*, which is present in suitable areas along the northern coast of Venezuela (i.e., Sierra de San Luis), but not on the peninsula itself. The lowlands of the peninsula, as well as the Istmo de los Médanos, the sandy spit of land connecting it to the "mainland", are apparently inhospitable for either species (see photograph in Romero, 1989).

Limited additional autecological information is available for the specimens collected by the Smithsonian Venezuelan Project. All six specimens were collected with a bait of sardines and rolled oats. Five were taken in snap traps, and one in a live trap. Four were encountered at tree bases (one of those in an area of ferns), one on a log, and one under a log in leaf litter. All five individuals taken in cloud forest were described as being in a "moist" site, and the one from thorn forest was near a stream. All were captured on ridge sides. Stomach contents included brown meal (adults), creamy fluid (one adult), and gray meal (a juvenile). Two adult males had large testes (18 × 7 mm; 17 × 9 mm), but two other adults collected the same week had much smaller ones (9 × 5 mm; 8 × 6 mm). The juvenal male (age class 1) had

testes measuring 6×4 mm. No reproductive information is available for the lone female. Mites were collected from all four adult males: one had both chiggers on its ears and brown mites on the body; another had chiggers on the ears and inside the hind legs; anopluran lice were also present on one of the mite-infested males. No parasites were found on the adult female, but the lone juvenile (a male, collected in a different habitat) had Siphonaptera and Anoplura on it.

CONSERVATION STATUS: Given the available natural history information, it appears that *Heteromys oasicus* currently inhabits a miniscule area. Because *H. anomalus* is known from the Sierra de San Luis on the adjacent "mainland", the presence of the new species is very unlikely outside mesic areas of the Península de Paraguaná. Thus, at most, its distribution encompasses ca. 22–25 km² (the approximate area above 200 m associated with Cerro Santa Ana and Monte Cano). More likely, the area with viable populations is much smaller, restricted to the higher (evergreen) slopes of Cerro Santa Ana (generally above 550 m), riparian depressions on the lower slopes of Cerro Santa Ana, and the lone significant stream on Monte Cano. The area above 550 m on Cerro Santa Ana extends only approximately 3 km². Although the area above 200 m along the Fila de Monte Cano is much greater, the distribution of semideciduous vegetation along the watercourse there (which *H. oasicus* inhabits) is extremely limited. Such restrictions probably make *Heteromys oasicus* one of the most narrowly endemic species of mammals in the world, and certainly in Venezuela (arguably even more so than *Lonchorhina fernandezi*, *Marmosops cracens*, *Neusticomys mussoi*, or *Podoxymys roraimae*; see Soriano and Ochoa-G., 1997; Linares, 1998).

Fortunately, these critical habitats for *H. oasicus* are currently protected as the Monumento Natural Cerro de Santa Ana (Bisbal-E., 1990) and the Reserva Biológica Monte Cano (Romero, 1989; Markezich and Taphorn, 1994). Concomitant with the declaration of the Monumento Natural in 1972 (part of the Venezuelan governmental system of protected areas), human presence on Cerro Santa Ana decreased along with a drastic re-

duction in hunting (of game species, especially rabbits, *Sylvilagus floridanus*; armadillos, *Dasybus novemcinctus*; and brocket deer, *Mazama gouazoubira*; Bisbal-E., 1990). Likewise, the species' habitat on Monte Cano is protected in a nongovernmental biological reserve managed by INFALCOSTA, a partnership between the Universidad Nacional Experimental Francisco de Miranda (in Coro) and local communities (M. Bevilacqua, in litt.; A. Martino, in litt; the reserve was formerly managed by BIOMA, see Romero, 1989; Markezich and Taphorn, 1994). The largest immediate threat to preservation of the natural vegetation on Cerro Santa Ana and Monte Cano is probably grazing by free-ranging domestic goats, which defoliate native vegetation on the slopes, causing an acceleration of natural erosional processes (Bisbal-E., 1990; Markezich and Taphorn, 1994). Additionally, on Monte Cano, small-scale gathering of wood and ornamental plants also occurs, the construction of infrastructure for tourism is planned, and small-scale mining projects are forthcoming (Romero, 1989; J. Ochoa-G., in litt.).

Heteromys anomalus (Thompson, 1815)
Caribbean Spiny Pocket Mouse

DISTRIBUTION: Distributed along the Caribbean coast of Colombia and Venezuela (east of the Río Atrato), in the upper Río Magdalena Valley, and up to middle elevations on the slopes of the Sierra Nevada de Santa Marta, Serranía de Perijá, Cordillera de Mérida, and other coastal ranges; also inhabits the Caribbean islands of Trinidad, Tobago, and Margarita (figs. 1, 5; Anderson, 1999; Williams et al., 1993; appendices 1 and 2). The species typically ranges from sea level to 1500–1600 m. The lone confirmed locality above that elevation is on the Macizco de Boconó (2430 m), an isolated massif close to the main body of the Cordillera de Mérida, where several mammals show atypical elevational distributions (Soriano et al., 1990). The species is notably absent from the locality Monte Zerpa (at 2160 m near the city of Mérida), which probably represents the small-mammal community in the Venezuelan Andes most completely known (Díaz de Pascual, 1988, 1994).

With regard to the species' distribution in Colombia, Alberico et al. (2000) miscited Anderson (1999), incorrectly reporting this species for the Departamento de Boyacá, while missing its documented presence in several departamentos (Atlántico, Bolívar, Cesar, La Guajira, and Sucre) and from the Serranía de Perijá. The specimen newly reported here from Huila, Colombia (MVZ 113950, locality 16, 17.5 km SE Villavieja, 1600 ft [488 m]), represents a significant range extension in the Magdalena Valley ca. 130 km to the SSW of the southernmost previous records, and the first for the Departamento de Huila.

In western Venezuela, collection of *Heteromys anomalus* has been especially common in piedmont areas. The specimens reported here expand the confirmed distribution of the species in the Serranía de Perijá, the Andean piedmont, and the western llanos. Furthermore, they confirm the species' presence from the Sierra de San Luis in Estado Falcón (compare with localities plotted by Linares, 1998). I do not know the basis of localities from western Venezuela plotted by Linares (1998) but not included in the present revision; they may derive from small Venezuelan museums that I did not visit (see Lew and Ochoa, 1993; Bisbal-E. and Sánchez-H., 1997). Utrera et al. (2000) reported the capture of 15 individuals of *H. anomalus* from seven localities in the western llanos. Although I have not examined any of their vouchers, they probably represent important new records of *H. anomalus*. However, Soriano and Clulow (1988) were the first to report the species from the western llanos (Hacienda Las Matas, 40 km SE Barinas, 270 m), contra Utrera et al. (2000: 539). This locality was not plotted by Linares (1998), but the specimens were confirmed by Anderson and Soriano (1999).

The species' distribution in northcentral and northeastern Venezuela (out of the geographic scope of the current work) currently remains unclear, as many records reported by Handley (1976) and plotted by Linares (1998) do not really represent *Heteromys anomalus* (Anderson, unpubl.). However, I have examined all specimens reported in this paper and vouch for their identity. Future

work will revise the genus in the rest of Venezuela.

DIAGNOSIS: A medium-to-large species of *Heteromys* with adults showing the following combination of characters: plantar surface of hind feet naked; dorsal pelage typically pale brown strongly grizzled with thin ochraceous hairs intermixed among spines, but occasionally almost uniformly dark drab-gray (in wet lowlands of Zulia and in the Cordillera de Mérida); no lateral ochraceous band present on flanks; tail typically strongly bicolored and long relative to body size; ears very large relative to body size, and characteristically rounded; pelage usually harsh and spiny, but often softer in montane regions; P4 with straight, moderately deep fold in anterior border of posterior loph; optic foramen small, with exterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point, then ascending dorsally to rejoin crest near its posterior termination; braincase narrow and strongly ridged; temporal fossae well excavated; interorbital region strongly constricted.

COMPARISONS: Externally, *Heteromys anomalus* is typified by its very large ears. Most populations are pale, with strongly grizzled dorsal pelage, in contrast to the dark brown or dark gray pelage of *H. nelsoni*, *H. oresterus*, *H. australis*, *H. teleus*, and species of the *H. desmarestianus* complex. Although members of the *H. desmarestianus* complex show an infusion of ochraceous hairs, producing a grizzled effect (Anderson, 1999; Anderson and Jarrín-V., 2002), those species are not nearly as strongly grizzled as the typical pale, strongly grizzled populations of *H. anomalus*. *Heteromys anomalus* differs from *H. gaumeri* by the haired plantar surfaces of the hind feet of the latter.

Cranially, *Heteromys anomalus* has a narrow, flat braincase (in sharp contrast to the wide, inflated braincase of *H. australis*). Its rostrum is neither as long and thin as the rostrum of *H. oresterus* nor as massive as that of *H. nelsoni*. It can be separated from species of the *H. desmarestianus* complex by: placement of parietomastoid suture, which dips well ventral to parietal crest posterior to its widest point and then ascends dorsally to rejoin crest near its posterior termination;

straight, deep fold in anterior border of posterior loph of P4; and especially small optic foramen. In contrast to *H. gaumeri*, *H. anomalus* has a large, anteriorly rounded postalar fissure. The zygomatic arches of *H. anomalus* are not as wide as those of *H. teleus*. See Comparisons section under *H. oasicus* for comparisons with that similar species.

NATURAL HISTORY: Despite the many records, little has been published regarding the natural history of *Heteromys anomalus* in Colombia and western Venezuela. Because of the presence of another species of the genus in eastern Venezuela (Anderson, unpubl.), the data reported for *H. anomalus* by Rood (1963), Rood and Test (1968), Handley (1976), and Valdez et al. (1985) do not correspond to that species alone. General vegetation maps show that collection localities for *H. anomalus* in Colombia and western Venezuela not only fall into regions that support evergreen forests, but also into areas harboring deciduous forests (IGAC, 1962, 1988b; DCN, 1977d). However, precise habitat information is lacking for the vast majority of collection localities, and some specimens from areas dominated by deciduous forests may have been captured in moister sites along streams. The species has been found in remnant forests and secondary scrub habitats in agricultural areas (e.g., Philip Hershkovitz field notes for Caracolicito, locality 8; Voss, 1991 for Misión Tukuko, locality 97). In one dry region dominated by nonforested vegetation, *H. anomalus* is present in gallery forests (Oliver Pearson field notes for Villavieja, locality 16). All records from the *llanos* (natural tropical savannas) with habitat data indicate the species' presence only in gallery forests and not in the open savanna (Soriano and Clulow, 1988; see also August [1984] and Utrera et al. [2000] for unconfirmed records).

Published reports and field notes provide some ecological data for *Heteromys anomalus* in western Venezuela. The species and its habit of transporting seeds in its cheekpouches figures in the folklore of the Perijá region (see photograph published by Pirlot, 1963: 201), where it is known by the indigenous name *maiuja* (Méndez-A., 1953) or *maiusa* (Pirlot, 1963). At Kunana (locality 94, Estado Zulia), *H. anomalus* was captured in both

forest and secondary growth (Méndez-A., 1953: 195). Similarly, *H. anomalus* was found in forested regions around Kasmara (locality 96, also in Zulia), among shrubs, below fallen trees, and near rocks; two specimens were even taken in the Kasmara biological station, but—despite significant effort—the species was not collected in banana plantations there (Pirlot, 1963). Specimens from El Panorama (locality 90, Zulia) were taken “under *mayas* [wild pineapple] and thorny shrubs which form hedgelike borders to the trails” that traverse that arid region dotted by spring-fed ponds (Osgood, 1912: 55). At Misión Tukuko (fig. 12; locality 97, Zulia) *H. anomalus* was most frequently captured in disturbed forests (where canopy trees remained but the understory had been removed and planted with coffee; Voss, 1991). However, the species was also encountered at that site in various secondary habitat types (such as overgrown orchards and small vegetated patches along streams), but not in open anthropogenic grasslands (Voss, 1991; Robert S. Voss, Helen Kafka, and Isa Torrealba field notes). In contrast to the information from sites in Zulia (where *H. anomalus* tolerated secondary growth in addition to inhabiting forests), the species was only captured in undisturbed evergreen forests (both along ridges as well as in more mesic habitats beside a stream) at Finca El Jaguar (locality 85, Estado Yaracuy), not in grassy pastures with fallen tree trunks or in thickets of mesic secondary growth (Robert S. Voss and Hernán G. Castellanos field notes). Both at Misión Tukuko and Finca El Jaguar, it was captured in both Sherman live traps and in snap traps, almost always on the ground or on downed logs or lianas less than 1 m above the ground (Robert S. Voss and colleagues field notes). A synthetic analysis of habitat information provided by all collectors would supply valuable information on the species, but has not yet been accomplished. Habitat information reported for *H. anomalus* by Handley (1976) should be re-evaluated once the genus is revised in the rest of Venezuela.

CONSERVATION STATUS: This widely distributed species is one of the more commonly collected small nonvolant mammals in northern Venezuela (Linares, 1998). In some cir-



Fig. 12. Landscape at Misión Tukuko (locality 97; Estado Zulia). *Heteromys anomalus* was frequently trapped in the disturbed forests in the background (as well as in regenerating thickets and small patches of vegetation along streams), but never in the open anthropogenic pastures in the foreground. Photographed in July 1986 by Robert S. Voss.

cumstances, it survives in forest remnants in low-intensity or “subsistence” agricultural regions (Adler et al., 1997; unconfirmed records in Utrera et al., 2000; see also Natural History). However, at other localities (e.g., Finca El Jaguar) it was restricted to undisturbed forests. Although widely collected, *Heteromys anomalus* evidently varies greatly in its local abundances, being found only in moderate numbers at some sites (e.g., Durant and Díaz, 1995), but at other localities representing one of the most frequently captured small mammals (e.g., Ochoa et al., 2001). Because collection efforts and protocols varied tremendously, numbers of specimens examined (see appendix 1) should not be taken to represent relative densities among sites. *Heteromys anomalus* has been collected in several national parks in both Colombia and Venezuela. Thus, its conservation outlook is favorable, but the species probably has suf-

fered local extirpation in many heavily disturbed areas.

Heteromys australis Thomas, 1901
Southern Spiny Pocket Mouse

DISTRIBUTION: Distributed from eastern Panama south to extreme northwestern Ecuador, and throughout much of the Colombian Andes (Anderson, 1999; Anderson and Jarrín-V., 2002). A disjunct population is also known from the Uribante drainage of the Cordillera de Mérida in western Venezuela (Anderson and Soriano, 1999).

DIAGNOSIS: A medium-sized species of *Heteromys* with adults showing the following combination of characters: plantar surface of hind feet naked; dorsal pelage dark gray to blackish; no lateral ochraceous band present on flanks; tail strongly bicolored in most populations but uniformly dark in some (es-

pecially on Pacific coast near Buenaventura, Colombia); ears small relative to body size; pelage harsh and spiny in lowland regions, but typically soft in mountains; P4 with straight, moderately deep fold in anterior border of posterior loph; optic foramen small, with exterior border formed by strong bar of bone; braincase wide and distinctly inflated, parietal and temporal crests moderately developed; temporal fossae moderately excavated; interorbital region wide.

COMPARISONS: *Heteromys australis* has dark gray or blackish dorsal pelage, in contrast to *H. anomalus*, *H. oasicus*, *H. gaumeri*, and members of the *H. desmarestianus* complex. *Heteromys nelsoni*, *H. oresterus*, and *H. teleus* are quite similar to *H. australis* externally, and are best separated using cranial characters. Cranially, *H. australis* has a wide, inflated braincase not found in other species. Its rostrum is neither as long nor as thin as that of *H. oresterus*. In overall size, it is dwarfed by *H. nelsoni*, which also has a more massive rostrum. *Heteromys australis* differs from *H. teleus* by its wider interparietal, narrower zygomatic arches, and narrower rostrum (Anderson and Jarrín-V., 2002). Like *H. anomalus*, it can be separated from species of the *H. desmarestianus* complex by a straight, deep fold in the anterior border of the posterior loph of P4 and an especially small optic foramen. Its inflated braincase best separates it from *H. anomalus*, but see also Anderson (1999) and Anderson and Soriano (1999) for further comparisons with that species. In contrast to *H. gaumeri*, *H. australis* has a large and anteriorly rounded postalar fissure.

NATURAL HISTORY AND CONSERVATION STATUS: Whereas *Heteromys anomalus* can survive in some agricultural settings, *H. australis* is evidently restricted to intact and only moderately disturbed tropical forests (Anderson, 1999; Anderson and Jarrín-V., 2002). Although large expanses of lowland habitat currently exist for the species in the Chocó of western Colombia and extreme northwestern Ecuador (IAvH and Etter-R., 1998; Sierra, 1999), the Andean distribution of the species has suffered much greater habitat destruction and fragmentation (Anderson, 1999; Anderson and Jarrín-V., 2002). The only known locality of the species in Vene-

zuela lies adjacent to the Embalse Uribante (a reservoir), in an area predominated by agriculture (P. Soriano, in litt.; J. Ochoa-G., in litt.; Anderson and Soriano, 1999). Thus, the species' current range in the country is unclear but probably restricted to forested montane western regions.

DISCUSSION

MORPHOLOGICAL DIFFERENTIATION OF *HETEROMYS OASICUS*

Morphometric analyses indicate that *Heteromys oasicus* is considerably smaller than the widespread *H. anomalus*, to which it is probably very closely related. Because no fossil heteromyines are known from South America (Marshall et al., 1982; Wahlert, 1993), it is difficult to reconstruct the body size of their most recent common ancestor and thus determine the direction of change in body size. Nevertheless, two lines of evidence suggest that *H. oasicus* represents a dwarf. First, all other species in the genus are larger than *H. oasicus*, while the body size of *H. anomalus* (its likely sister species) is average for the genus. Second, geographic samples of *H. anomalus* display relatively constant overall body size, even though some of them represent insular populations.

The results raise the hypothesis that morphological differentiation between *Heteromys oasicus* and *H. anomalus* (at least in those aspects of skull size and shape that can be quantified with linear measurements) is restricted to consequences of allometric growth. In addition to size differences, the observed shape differences may simply be concomitant with differential adult sizes, due to the constraints of allometric growth patterns. Explicit modeling of the allometric growth vector and further morphometric analyses are necessary to properly characterize the basis of the shape differences present between adults of the two species (Burnaby, 1966; Thorpe, 1983a, 1983b, 1988; Rohlf and Bookstein, 1987; Voss et al., 1990; Voss and Marcus, 1992; Bekele et al., 1993).

While the original geographic context of this morphological differentiation is unknown, it seems likely that it occurred when populations of *Heteromys anomalus* (or its

most recent common ancestor with *H. oasicus*; Hennig, 1966) on the Península de Paraguaná became isolated from those present across the rest of the Caribbean coast of Venezuela. *Heteromys oasicus* currently appears restricted to limited areas of mesic vegetation on the peninsula, principally cloud forest near the summit of Cerro Santa Ana and mesic vegetation patches on Monte Cano. Most of the peninsula and the spit of land connecting it to the “mainland” are currently covered by thorn forests and other xeric vegetation apparently uninhabitable for either species.

If a vicariant event led to the differentiation of this species from populations of *Heteromys* present across the Caribbean coast of South America, several geographic scenarios are possible. For example, contraction of mesic forested vegetation (similar to current conditions) tens of thousands of years ago may have rendered populations on Paraguaná isolated from those on the rest of the mainland, even while the peninsula maintained a broad connection to the rest of the continent (Markezich et al., 1997). Alternatively, morphological differentiation (here interpreted as speciation) could have occurred during temporary separation of the Paraguaná landmass as an island due even to slight fluctuations in sea level during an antiglacial period. Interestingly, specimens of *H. anomalus* from Isla Margarita off Venezuela’s northeastern coast are not dwarfed (ONL = 34.13–35.15 mm for EBRG 15081 and USNM 405982, males in age class 4; MTR = 5.56, PB = 12.14 for MHNLS 199, a female in age class 5 with slightly broken skull). Similarly, only some populations from Trinidad are smaller than typical body size in *H. anomalus*, and those only moderately so. These two islands lie on the continental shelf of South America and were likely connected to the continent during the last glacial maximum, or at least during some Pleistocene glacial cycles (Koopman, 1958; Smith and Genoways, 1974; Handley, 1976; Voss, 1991). Similar in many ways to Cerro Santa Ana but much larger, the Serranía de La Macuira holds an isolated patch of cloud-forest vegetation on low peaks lying within a matrix of xeric vegetation on the Península de La Guajira in northeastern Colombia (Gar-

cés-Guerrero and de la Zerda-Lerner, 1994). Yet, the lone specimen of *H. anomalus* known from the serranía is typical in size for *H. anomalus* (MTR = 5.13, IW = 9.21, IL = 4.72 for IND-M 5924, adult in age class 5 of unknown sex; measurements taken by Marcela Gómez-Laverde on broken skull).

These data intimate that the selection pressures that produced such a small pocket mouse on Paraguaná may be related to the extremely small habitable area there. Such regions are much smaller than those available on Isla Margarita, Trinidad, or the Serranía de La Macuira (even though the total area of Paraguaná is larger than that of Margarita, for example). The small areal extent of islands and restricted habitat types frequently produces a cascade of demographic and community-level changes for species there, leading in many cases to evolutionary changes in body size (Foster, 1964; Case, 1978; Lawlor, 1982; Kalko and Handley, 1994; Marquet and Taper, 1998; Anderson and Handley, 2002). Typically, small mammals evolve larger size following insularization (Heaney, 1978; Lomolino, 1985; Roth, 1992), making this case of dwarfism even more noteworthy and calling for autecological studies comparing populations of *H. oasicus* with mainland populations of *H. anomalus*. Future inventories should target other low peaks in arid regions of Colombia and Venezuela holding small areas of mesic vegetation, for additional potentially differentiated taxa of *Heteromys* and other groups. In addition, future work investigating phylogeographic patterns of genetic divergence among populations of the two species would lend critical insight into the evolutionary history of *H. oasicus*.

ENDEMISM ON PARAGUANÁ

Although biological knowledge of the Península de Paraguaná remains incomplete even at the inventory level, available data document a few other endemic forms, attesting to the peninsula’s semi-insular nature and peculiar history. The species composition of mammals, birds, reptiles, and amphibians is now moderately well known on Paraguaná (Barnes and Phelps, 1940; Bisbal-E., 1990; Mijares-Urrutia et al., 1995; Mijares-Urrutia

and Arends-R., 1997, 2000). Most species of these groups present on the peninsula are restricted to xeric thorn scrub or deciduous forests in the lowlands, and extend to similar habitats on the main body of the continent (Barnes and Phelps, 1940; Bisbal-E., 1990; Linares, 1998; Mijares-Urrutia and Arends-R., 2000). A moderate percentage of the species found in dry lowland habitats also ascend Cerro Santa Ana to mesic vegetation types (Bisbal-E., 1990). However, of all terrestrial vertebrate species listed by Bisbal-E. (1990) from Cerro Santa Ana, the new species of *Heteromys* is the only one restricted to cloud forests and other mesic (evergreen) montane vegetation. Two mammals (*Dasyus novemcinctus* and *Proechimys guairae*) and three birds (*Aramides axillaris*, *Ortalis ruficauda*, and *Seiurus noveboracensis*) were found in both deciduous and evergreen forests on the *cerro*, but not in lower xerophytic areas. Likewise, four birds (*Arremonops tocuyensis*, *Seiurus aurocapillus*, *Setophaga ruticilla*, and *Thamnophilus doliatus*) and one lizard (*Mabuya mabouya*) were restricted to deciduous forests on Cerro Santa Ana (Bisbal-E., 1990). Continued inventory work should examine the possibility that these populations are isolated on the *cerro* and may be evolutionarily distinct from congeners on the main body of South America.

No other currently recognized mammalian species is endemic to the peninsula (Soriano and Ochoa-G., 1997; Linares, 1998), but one other vertebrate and at least one plant are. Before the present study, the only recognized endemic mammalian taxon was a highly differentiated subspecies of a mormoopid bat (*Pteronotus parnellii paraguayensis*), which inhabits dry lowland areas of Paraguaná (Linares and Ojasti, 1974; Martino-G. et al., 1997). A subspecies of the yellow warbler (*Dendroica petechia paraguayanae*) is considered endemic to the peninsula by some (Romero, 1989), but the distinctiveness of this avian subspecies is questioned by others (Klein and Brown, 1994). A snake, *Leptodeira bakeri*, is only known from dry areas on Paraguaná and the nearby island of Aruba (Mijares-Urrutia et al., 1995). The recently described gecko *Lepidoblepharis montecanoensis* evidently represents the only other vertebrate species currently considered en-

demic to the peninsula, confined to small forested areas on Paraguaná (Markezich and Taphorn, 1994). Although *Heteromys oasicus* is likely sympatric with this lizard on Monte Cano, *L. montecanoensis* is tolerant of semideciduous forests along lowland watercourses where *H. oasicus* is not known. Perhaps even more restricted than *H. oasicus*, the palm *Geonoma paraguayensis* is definitively known only from Cerro Santa Ana (Bisbal-E., 1990), but its specific status is in question relative to samples of the genus from the Sierra de San Luis and elsewhere on the “mainland” (Stauffer, 1999). Additionally, several other mammalian taxa appear to be differentiated on the peninsula (J. Molinari, in litt.), but detailed taxonomic comparisons of these forms with their congeners have not been undertaken. Thus, we cannot yet judge the true evolutionary context in which the striking case of *H. oasicus* stands. Future work should include more inventories on Paraguaná, genetic studies comparing Paraguaná populations with each other and with ones from the Venezuelan “mainland”, and detailed revisionary studies of the specimens already in existence.

ACKNOWLEDGMENTS

I am pleased to dedicate this work to my Venezuelan colleagues, who graciously welcomed me to their museums and shared their knowledge of spiny pocket mice and the biogeography of northern South America in the course of many memorable discussions. The following curators and collection managers allowed me access to and/or provided loans of specimens under their care: Nancy B. Simmons and Robert S. Voss (AMNH); Ted Daeschler (ANSP); Suzanne B. McLaren (CM); Pascual Soriano (CVULA); Francisco Bisbal and Javier Sánchez (EBRG); Lawrence R. Heaney, Bruce D. Patterson, and William T. Stanley (FMNH); Alberto Cadena (ICN); H. Chiriví, Fernando Gast, Yaneth Muñoz-Saba, and Vicente Rueda (IND-M/IAvH); Robert M. Timm and Thor Holmes (KU); James Dines (LACM); Roger Pérez-Hernández (MBUCV); Marisol Aguilera (MCNUSB); Maria E. Rutzmoser (MCZ); Daniel Lew and Belkis Rivas (MHNLS); Hermano Roque Casallas and Arturo Rodrí-

guez (MLS); James L. Patton and Barbara Stein (MVZ); Candace McCaffery and Laurie Wilkins (UF); Philip Myers and Priscilla K. Tucker (UMMZ); Michael D. Carleton, Robert D. Fisher, Linda K. Gordon, the late Charles O. Handley, Jr., James G. Mead, and Richard W. Thorington, Jr. (USNM); Michael Alberico (UV); and Holly McEntee and E. Elizabeth Pillaert (UWZM). I thank Alberto Fernández-Badillo and Richar Visbal (Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay) for access to specimens of *Heteromys* from eastern Venezuela not reported here, but which gave me a broader context for understanding the current issues at hand. Amelia Díaz de Pascual, Pedro Durrant, Daniel Lew, Holly McEntee, Ángela Martino-G., Suzanne McLaren, José Ochoa-G., Oliver Pearson, Jaime Péfaur, Roger Pérez-Hernández, Suzanne Peurach, Adriana Ruiz-Espinoza, Pascual Soriano, Ángel L. Viloria, and Robert S. Voss responded with patience and critical assistance to my many queries regarding collection localities; Róger Pérez-Hernández, Mercedes Salazar, and Carmen Ferreira made their excellent series of Venezuelan topographic maps available to me at the Universidad Central de Venezuela. Before his death, Charles Handley encouraged my investigation and description of this taxon, which he had first identified as new to science. María Pía Bevilacqua, Miriam Díaz, and Ángela Martino-G. provided vegetational data on the Fila de Monte Cano and Cerro Santa Ana. Marcela Gómez-Laverde completed osteological preparation of the skull of the lone *H. anomalus* known from the Serranía de La Macuira and measured it at my request. Michael D. Carleton, Mark S. Hafner, Daniel Lew, José Ochoa-G., A. Townsend Peterson, Norman A. Slade, Robert M. Timm, and Robert S. Voss read portions of previous drafts of this manuscript and made helpful comments. This research was supported by a National Science Foundation Graduate Research Fellowship, the Thomas J. Dee Fund (Field Museum), the Panorama Society and the E. Raymond and Mary Hall Fund (University of Kansas), a Grant in Aid of Research (American Society of Mammalogists), and a Collection Study Grant and

Roosevelt Postdoctoral Research Fellowship (American Museum of Natural History).

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APPENDIX 1

GAZETTEER OF SPECIMENS EXAMINED FROM
PRINCIPAL STUDY AREA

Here I report all specimens of *Heteromys* examined from western Venezuela (west of the Depresión de Yaracuy) and all *H. anomalus* known to me from Colombia. Secondary information provided by sources other than the collector is included in brackets followed by the source. Localities are numbered to correspond to figure 5, where they are plotted, and are arranged here from north to south within secondary political division. For each locality, boldface indicates the place name to which geographic coordinates correspond. Coordinates are provided for only those localities that could be determined to within ca. 10 km. Most are accurate to within 5 km (approximately 2 minutes); the placement of “ca.” immediately before the coordinates indicates those accurate to an estimated 6–10 km. Museum catalog numbers for specimens examined follow each locality, using the abbreviations provided in Materials and Methods. See appendix 2 for specimens examined outside principal study area and appendix 3 for lists of measured specimens.

Heteromys anomalus (total 537)

COLOMBIA (total 230):

ANTIOQUIA

1. **Urabá, Río Currulao**, 50 m [8°00'N, 76°44'W, Hershkovitz, 1977], FMNH 70473.

2. **Caucasia, 12 km S** (Hacienda Barro), 250 m [7°53'N, 75°12'W, IGAC, 1989a; not Voss, 1991], USNM 449537, 449538.

ATLÁNTICO

3. **Ciénaga de Guájaro, Sabana Larga** [15 m, 10°37'N, 75°02'W, Hershkovitz, 1947], USNM 280209–280213.

BOLÍVAR

4. **San Juan Nepomuceno**, 167 m [9°58'N, 75°04'W, Hershkovitz, 1977], FMNH 69225–69235.
5. **Río San Pedro, Norosí**, Mompós [180 m, 8°38'N, 74°04'W, Hershkovitz, 1977], USNM 280298.

CESAR

6. **Pueblo Bello** [1067 m, 10°24'N, 73°39'W, Hershkovitz, 1947], USNM 280251–280253.
7. **El Salado** [430 m, 10°22'N, 73°29'W, Hershkovitz, 1947], USNM 280254–280269.
8. **Colonia Agrícola de Caracolicito**, Santa Marta, 400 m [10°18'N, 74°00'W, Hershkovitz, 1947], USNM 280214–280250.
9. Valledupar, **El Guaimaral** [140 m, Hershkovitz, 1947, who stated that El Guaimaral was located 5 km from El Orinoco; ca. 10°13'N, 73°23'W, for El Orinoco; Hershkovitz, 1960; not Hershkovitz, 1947; Voss, 1991; or Anderson, 1999], USNM 280270–280277.

CÓRDOBA

10. **San Andrés de Sotavento** [9°08'N, 75°32'W, Adler et al., 1997], UV 11239.
11. **Montería**, Granja Turipaná, 15 m [ca. 8°46'N, 75°53'W, Paynter, 1997], UV 8435, 9830–9031.
12. **Catival, upper Río San Jorge**, 120 m [8°17'N, 75°41'W, Hershkovitz, 1977], FMNH 69243–69256.
13. **Socorré, upper Río Sinú**, 100 m [7°51'N, 76°17'W, Hershkovitz, 1977], FMNH 69236–69239.

CUNDINAMARCA

14. Caparrapí, **Volcanes** [250 m, Hernández-Camacho, 1956; ca. 5°27'N, 74°31'W, IGAC, 1973; Anderson, 1999; not Hernández-Camacho, 1956; Voss, 1992; or Musser et al., 1998], ICN 409, 1827–1831, 1832 (holotype of *Heteromys anomalus hershkovitzi* [= no. 2701 of former Instituto Carlos Findlay]), 1833–1835, 1866; MLS 2173.
15. **Vereda El Callejón**, 350 m [ca. 4°18'N, 74°43'W, IGAC, 1989b], ICN 12575, 12576, 12882–12884.

HUILA

16. **17.5 km SE Villavieja**, 1600 ft [488 m; 3°03'N, 75°11'W; IGAC 1985a; near Quebrada Coscarrón and Quebrada Aceite; O. Pearson, in litt.], MVZ 113950.

LA GUAJIRA

17. **San Francisco**, 6000 ft [1829 m; but see Paynter, 1997, who gave approximately 1000 m; 11°00'N, 73°26'W, Paynter, 1997], MCZ B8359.
18. **Pueblo Viejo** [= El Pueblito], 8000 ft [2438 m; but see Todd and Carriker, 1922, and Paynter, 1997, who gave 2000 ft (610 m); 10°59'N, 73°27'W, IGAC, 1988a; Paynter, 1997; not Musser et al., 1998], MCZ B8072, B8074; USNM 85543; and **Pueblo Viejo**, Sierra Nevada de Santa Marta [same coordinates], CM 3178, 3182.
19. **San Miguel** [1700 m, 10°58'N, 73°29'W, Paynter, 1997], MCZ B8265.
20. **Mamorongo** [Mamorongo on skin tag; see Bangs, 1900], 3000 ft [914 m; ca. 10°57'N, 73°18'W, Paynter, 1997; see also Todd and Carriker, 1922, and note a Río Mamorongo to the west, a tributary of the Río Palomino; IGAC, 1988a; a locality at 3000 ft on the Río Mamorongo would have coordinates of ca. 11°02'N, 73°37'W], MCZ B8358.

21. **Las Marimondas**, E. Andes, Fonseca [1000 m, 10°52'N, 72°43'W, Hershkovitz, 1947], USNM 280293–280297.
22. **Villanueva**, Valledupar, 280 m [10°37'N, 72°58'W, Hershkovitz, 1947], USNM 280283–280292.
23. **Sierra Negra**, Villanueva, Valledupar, 1500 m [10°36'N, 72°55'W, Hershkovitz, 1960], USNM 280278–280282.
24. **Serranía La Macuira** [precise location within *serranía* not available], IND-M 5924.

MAGDALENA

25. Parque Nacional Natural Tayrona, **El Cedro**, 420 m [11°19'N, 74°01'W, Garcés-Guerrero and de la Zerda-Lerner, 1994; IGAC, 1975], ICN 9053–9055; IND-M 2783, 4178, 4885.
26. **Don Diego**, 5 m [11°15'N, 73°42'W, Paynter, 1997], FMNH 13234, 13235, 44864; and **Don Diego**, Santa Marta [same coordinates], CM 3121, 3125, 3126, 3131, 3144–3147, 3160.
27. **Buritaca** [near sea level, 11°15'N, 73°46'W, Paynter, 1997], AMNH 23318; FMNH 13233.
28. **Bonda** [approximately 150 ft (46 m), 11°14'N, 74°08'W, Paynter, 1997], AMNH 15352–15354; CM 838; **Bonda**, 100 m [same coordinates], LACM 56391.
29. **Mamatoca**, 100 ft [30 m; 11°14'N, 74°10'W, Paynter, 1997], AMNH 15351.
30. **El Líbano Plantation**, 500 ft [152 m; 11°13'N, 74°10'W; IGAC, 1975; Allen, 1904], AMNH 15349–15350.
31. **Masinga Vieja**, 500 ft [152 m; 11°12'N, 74°05'W; IGAC, 1975, given placement provided by Todd and Carriker, 1922; not Paynter, 1997; or Anderson, 1999], AMNH 15356.
32. **Onaca** [680 m, 11°11'N, 74°04'W, Paynter, 1997], AMNH 15355, 23632.
33. **Minca**, 2000 ft [610 m; 11°09'N, 74°07'W, Paynter, 1997], AMNH 15344–15346, 15493, 23320; CM 848; and **below Minca**, 1000 ft [305 m, same coordinates], AMNH 15347 (holotype of *Heteromys jesupi*), 15348.
34. Alto de Mira, **3 km W del Río Buritaca**, Sierra Nevada de Santa Marta, 1050 m [ca. 11°08'N, 73°54'W, IGAC, 1975; coordinates correspond to indicated elevation], ICN 13010.
35. **Palomino** [approximately 600 m, 11°02'N, 73°39'W, Paynter, 1997; see also Todd and Carriker, 1922], MCZ B8255–

B8258, B8260–B8264, B8351–B8357; USNM 85542.

36. **Río Frío**, 50 m [10°55'N, 74°10'W; Paynter, 1997], LACM 56392.
 37. **Olimpia**, 2500 ft [762 m; not located], AMNH 23319.

NORTE DE SANTANDER

38. **Río Tarrá, San Calixto** [approximately 200 m, 8°36'N, 73°01'W, Hershkovitz, 1947], USNM 280305, 280306.
 39. **Guamalito, El Carmen** [approximately 600 m, 8°34'N, 73°27'W, Hershkovitz, 1947], USNM 280299–280304.
 40. Corregimiento de La Donjuana, Hacienda **La Selva** [approximately 1100 m, ca. 7°45'N, 72°35'W, Paynter, 1997], MLS 2048, 2049.
 41. **Durania**, Finca La Palma [ca. 7°43'N, 72°40'W, IGAC, 1985b], ICN 10974.

SUCRE

42. **Colosó, Las Campanas**, 175–350 m [9°30'N, 75°21'W, Hershkovitz, 1977; Paynter, 1997], FMNH 69240–69242.

TOLIMA

43. **Honda**, Magdalena River, 600 ft [183 m; 5°12'N, 74°45'W, Paynter, 1997], AMNH 34593.
 44. **Chicoral, Coello River**, 1800 ft [549 m; 4°13'N, 74°59'W, Paynter, 1997], AMNH 32965.
 45. **Melgar** [430 m, ca. 4°12'N, 74°39'W, Paynter, 1997], ICN 4402, 4403.

VENEZUELA (total 307):

BARINAS

46. **27.5 km NW (by road) Barinitas** [ca. 8°52'N, 70°34'W; SAGCN, 1994a; ITMB, 1997], EBRG 3543.
 47. La Quinta, **0.5 km SW Altamira**, 697 m [8°50'N, 70°30'W; Handley, 1976; DCN, 1976b], EBRG 15090, 15099; USNM 442102, 442103.
 48. **Cerro Alto**, 2 km NW La Soledad, 1460–1600 m [8°50'N, 70°32'W; DCN, 1976b], CVULA I-5924, 5932, 5939; EBRG 22002–22004; and **Cerro Alto**, 3 km N La Soledad, 1500–1580 m [same coordinates], CVULA I-846, 924, 926, 1037, 1040–1042, 1044–1048, 1294.
 49. **Barragán**, Barinitas, 400–440 m [8°48'N, 70°27'W; DCN, 1975a], CVU-LA I-837, 904, 1161.
 50. El Palmar, N **Barinitas**, 1000 m [ca.

8°45'N, 70°25'W; Paynter, 1982], CVU-LA I-1049, 2329.

51. **3 km SW Barinitas**, Río Marginos [approximately 600 m, 8°45'N, 70°26'W; DCN, 1975a], MCNUSB I-415.
 52. **11 km by road E Barinitas** [250–500 m, ca. 8°41'N, 70°22'W; SAGCN, 1994a; ITMB, 1997], CM 78751.
 53. **Hacienda Las Matas**, 40 km SE Barinas, 270 m [8°25'N, 70°03'W; Soriano and Clulow, 1988], CVULA I-4015, 4048, 4297, 4346.

FALCÓN

54. Parque Nacional J.C. Falcón [= Parque Nacional Juan Crisóstomo Falcón], **Cerro La Danta**, N La Soledad, Sierra de San Luis, 1300–1470 m [11°14'N, 69°36'W; DCN, 1969; D. Lew, in litt.], MHNLS 9565–9568.
 55. **1.3 km SE San Joaquín**, Parque Nacional Sierra de Falcón [= Parque Nacional Juan Crisóstomo Falcón], 1200 m [11°12'N, 69°35'W; DCN, 1969], EBRG 21742.
 56. 5 km N, 13 km E Mirimire, near **La Pastora**, 122–170 m [11°11'N, 68°35'W; DCN, 1968; see also Handley, 1976], USNM 456322, 456323.
 57. 20 km S & 98 km E Maracaibo, **Hacienda Socopito** [= Río Socopito, 80 km NW Carora], 470–480 m [10°30'N, 70°44'W; Handley, 1976], EBRG 15105–15109, 16692–16696; USNM 442085, 442086, 442089–442095, 495323–495326, 495331–495334.

LARA

58. **El Blanquito**, 9 km [airline] SE de Sanare, Parque Nacional Yacambú, 1650 m [9°42'N, 69°37'W; DCN, 1975c; P. Soriano, personal commun.; see also Ochoa et al., 2001], CVULA I-2695, 2728, 2732, 2736, 2741–1743, 2750, 2754, 2755; **El Blanquito**, 17 km [by road] SE de Sanare, Parque Nacional Yacambú, 1600 m [same coordinates], CVULA I-6162; MCNUSB I-808–817, 852–856, 1455; **El Blanquito**, 17–18 km [SE by road] de Sanare, Parque Nacional Yacambú, 1500 m [same coordinates], EBRG 10302, 22728, 22729; and Parque Nacional Yacambú; [near **El Blanquito**; J. Ochoa-G., in litt.], 1500–1650 m [same coordinates], MBUCV I-4843, 4844, 4846–4848, 4850, 4851, 4856, 4859, 4864, 4865, 4867, 4882, 4906, 4990, 4991.
 59. **Aproximadamente 6 km de El Blanqui-**

to vía Sanare, Parque Nacional Yacambú, 1700 m [9°42'N, 69°39'W; DCN, 1975c; J. Ochoa-G., in litt.], EBRG 10611–10618, 10979.

60. 11 km [by road] SSW [SSE] Sanare, **La Pastora**, 1650 m [9°41'N, 69°39'W; DCN, 1975c], MHNLS 4919.

MÉRIDA

61. Capazón, **La Azulita**, 1000 m [8°43'N, 71°27'W; Paynter, 1982], CVULA I-1038, 1039, 1043, 1047; and **La Azulita**, 1135 m [same coordinates], FMNH 22170.
62. **El Vigía**, Hacienda El Roble, 150 m [ca. 8°38'N, 71°39'W; Paynter, 1982], CVULA I-894.
63. **Bejuquero**, W [NE] Zea; 15 km N Tovar, 600 m [8°27'N, 71°45'W; DCN, 1977b], CVULA I-256, 257.
64. **Hacienda La Trinidad, Caño Tigre**, 370 m [8°26'N, 71°46'W; DCN, 1977b]; “carreterra Zea-El Vigía, a 2 km de la ribera derecha del Río Escalante”, Amelia Díaz de Pascual and P. Durant, in litt.; see also Durant and Díaz, 1995], CVULA I-2528, 2529.
65. **8 km (by road) S Estánquez on road to Canaguá**, 1500 m [ca. 8°25'N, 71°32'W; DCN, 1977b], UWZM S.31419.
66. **La Cuchilla del Niño**, 2 km SW [NW] Zea, 1250 m [8°24'N, 71°47'W; DCN, 1977b], CVULA I-6021.
67. **Cucuchica**, 6 km E Tovar, 1200–1250 m [8°20'N, 71°42'W; DCN, 1977b], CVULA I-5971, 5986–5988, 5993, 6003, 6004, 6008, 6009, 6019; and **Cucuchica**, 8 km E Tovar, Finca Mesa Rica, 1250 m [same coordinates], CVULA I-6024.

PORTUGUESA

68. **La Trinidad** [140 m, 9°13'N, 69°28'W; DCN, 1970b], MCNUSB I-421.
69. **Tierra Buena** [100–250 m, 9°12'N, 69°31'W; DCN, 1975b], UF 13318.
70. **San Jorge**, Píritu, 100 m [9°06'N, 69°27'W; DCN, 1970b], UF 13319.
71. Cogollal, near **Guanarito** [<100 m, ca. 8°42'N, 69°13'W; DCN, 1971a], AMNH 266914.
72. **Cerro Sabana, Santa Lucía** [not located; multiple towns named Santa Lucía are present in Estado Portuguesa, and no Cerro Sabana is evident on my maps], UF 13320.

TÁCHIRA

73. **San Pedro del Río**, 12 km [by road] W [NNW] Michelena [500–1000 m, 8°00'N, 72°16'W; DCN, 1977a], CVULA I-6196.

74. **Quebrada Las Lapas**, Río Potosí [= Río Puya], Uribante, 1050 m [7°58'N, 71°41'W; DCN, 1976a; now submerged in the Represa/Embalse Uribante at this elevation, the Quebrada Las Lapas was a tributary of the Río Puya; J. Péfaur, in litt.], CVULA I-2516.

TRUJILLO

75. 25 km NW Valera, near **Agua Viva**, 95 m [9°33'N, 70°39'W; SAGCN, 1996b; see also Handley, 1976], USNM 372506.
76. 23 km NW Valera, **Agua Santa**, 90 m [9°32'N, 70°39'W; SAGCN, 1996b; see also Handley, 1976], EBRG 15050, 15051, 15057, 15058, 15062, 15063, 16682; USNM 371021, 371023, 371025, 371027, 371030, 371031, 371035, 495290.
77. 30 km NW Valera, near **El Divide**, 90 m [9°29'N, 70°44'W; SAGCN, 1996b; see also Handley, 1976], USNM 372502–372505, 495292.
78. 49 km WNW Valera, near **Santa Apolonia**, 27 m [9°28'N, 71°04'W; Handley, 1976], EBRG 15078; USNM 372508.
79. **14 km SE Agua Viva**, 300 m [9°27'N, 70°33'W; SAGCN, 1996b; ITMB, 1997], MBUCV I-1824, 1825.
80. **5 km E Motatán**, 330 m [9°24'N, 70°33'W; DCN, 1976c]; KU 120258.
81. **2 km E Motatán**, 370 m [9°24'N, 70°35'W; DCN, 1976c], KU 120257.
82. 10 km WNW Valera, **Isnotú**, 930 m [9°22'N, 70°42'W; SAGCN, 1996b], EBRG 15066; USNM 371033, 370134.
83. **Macizo de Guaramacal, 6 km SE Bokonó**, 2430 m [9°15'N, 70°12'W; DCN, 1977c; Soriano et al., 1990], CVULA I-2960.

YARACUY

84. **19 km NW Urama**, km 40 [25–60 m, 10°33'N, 68°27'W, near border with Falcón; SAGCN, 1994b; see also Handley, 1976], EBRG 15076, 15077; USNM 372497, 372498, 372500, 374691.
85. **Finca El Jaguar**, ca. 15 km NNW Aroa, 680 m [10°32'N, 68°59'W; DCN, 1971b; not Voss, 1991], MHNLS 7215, 7238, 7452; **Finca El Jaguar**, 16 km NW de Aroa, 750–800 m [same coordinates], EBRG 21750, 22344; **Finca El Jaguar**, 21 km (by road) NW Aroa, 700 m [same coordinates], AMNH 257219–257221, 257223, 257224; MHNLS 8100, 8103, 8109, 8116; and **Finca El Jaguar**, Que-

- brada El Charal, 700 m [same coordinates], EBRG 18903, 20699.
86. **Miñas de Aroa**, 20 km NW San Felipe, 407 m [10°25'N, 68°54'W; Handley, 1976], USNM 495320.
87. **Lagunita** de Aroa, 1820 ft [555 m; 10°23'N, 68°55'W; SAGCN, 1994b], AMNH 32082.
88. **Urachiche**, Río Tejar [approximately 500 m, 10°10'N, 69°01'W; DCN, 1976d], MCNUSB I-416–420.

ZULIA

89. 40 km NW La Paz, **Cerro Azul** [= 18 km N, 56 km W Maracaibo, Hacienda Rodeo], 80 m [10°51'N, 72°16'W; Handley, 1976; Voss, 1991; DCN, 1970a], EBRG 16697; USNM 442098, 442099, 495337.
90. **El Panorama**, Río Aurare [= Río Anau-re; near sea level, 10°40'N, 71°25'W; Paynter, 1982; Osgood, 1912], FMNH 18622, 18623 (holotype of *Heteromys anomalus brachialis*), 18624–18627.
91. **Cuenca Río Palmar, Río Lajas**, 700 m [ca. 10°28'N, 72°32'W; SAGCN, 1996c], EBRG 17233.
92. Serranía de Perijá, **Río Cogollo**, 350 ft [107 m; 10°15'N, 72°30'W; Paynter, 1982], FMNH 22167–22169.
93. **Río Arajamo** [tributary of Río Apón], Serranía de Perijá, 1000 m [ca. 10°12'N, 72°46'W; SAGCN, 1996c; DCN, 1974b; Río Arajamo is a tributary of the Río Apón and must lie near the approximate coordinates presented here, which are taken at the indicated elevation; J. Péfaur, in litt.], CVULA I-1507, 1508.
94. **Kunana** [= Cunana], Río Negro, Serranía de Perijá, 1100 m [10°03'N, 72°48'W; DCN, 1974b], MHNLS 65, 71–74, 76.
95. **Hacienda Medellín**, al pie de Sierra Perijá, 150 m [9°57'N, 72°43'W; DCN, 1974a], MBUCV I-297
96. 10 km S, 18 km W Machiques, **Kasmera** [= 21 km SW Machiques], 270–273 m [9°57'N, 72°45'W; DCN, 1974a; not Handley, 1976], EBRG 150102–15104, 16691; USNM 442075, 442077, 442078, 442080, 442081, 442083, 495322; **Kasmera**, 37 km [by road] WSW Machiques, 320 m [same coordinates], KU 120259; and **Kasmera**, Serranía de Perijá, 220–250 m [same coordinates], MBUCV I-296, 1230, 1780, 1832, 1833.
97. **El Tucuco** [= Los Ángeles del Tucuco], 46 km SSW Machiques, 300–400 m [9°51'N, 72°49'W; DCN, 1974a; not Voss, 1991], CVULA I-1890, 5698; **Misión Tukuko**, 200–400 m [same coordinates], MHNLS 7711, 7724, 7728, 7739, 7772, 7773, 7776–7778, 7781, 7800–7803, 7708, 7709, 7806, 7811, 7816; USNM 448546–448561, 448754–448757; and **El Tukuko**, Quebrada Manantial, 260 m [same coordinates], MHNLS 6963, 6964, 6890, 6891.
98. **45–48 km WNW Encontrados**, El Rosario, 37–54 m [9°10'N, 72°40'W; SAGCN, 1996c; see also Handley, 1976], EBRG 15100, 15101, 16698; USNM 442104, 442107, 495340, 495341.

Heteromys australis (total 1)

VENEZUELA (total 1):

TÁCHIRA

99. **Presa La Honda, 10 km SSE Pregone-ro**, 1100 m [7°57'N, 71°42'W; Anderson, 1999; DCN, 1976a; SAGCN, 1996a; the Presa (= Quebrada) La Honda was a small tributary of the Río Uribante (= Río Puya) and now flows into the Represa/Embalse Uribante; it is above lake level at this elevation; P. Soriano, in litt.], CVULA I-3503.

Heteromys oasicus (total 10)

VENEZUELA (total 10):

FALCÓN

100. **Montecano** [= Monte Cano], Pueblo Nuevo, Paraguaná [approximately 200–250 m, 11°57'N, 69°59'W; DCN, 1974c], EBRG 20697, 20698.
101. 49 km N, 33 km W of Coro, **Moruy**, 90 m [11°50'N, 69°59'W; DCN, 1974c; see also Handley, 1976], USNM 456324.
102. 49 km N, 32 km W of Coro, **Cerro Santa Ana** [= 15 km SSW Pueblo Nuevo], 550–615 m [11°49'N, 69°57'W; DCN, 1974c; see also Handley, 1976, and Bisbal-E., 1990], EBRG 15110, 15111; USNM 456325 (holotype of *Heteromys oasicus*), 456327, 495338; and **Cerro Santa Ana**, Península de Paraguaná, 420–550 m [same coordinates], EBRG 3705, 15984.

APPENDIX 2

OTHER SPECIMENS EXAMINED (OUTSIDE PRINCIPAL STUDY AREA)

See Gazetteer (appendix 1) for specimens examined from principal study area.

***Heteromys anomalus* (total 157): TRINIDAD AND TOBAGO (72): TRINIDAD:** Bush Bush Forest, Nariva Swamp, AMNH 186626, 186627, 186631, 186633, 186634, 186636, 186639, 186641, 186643, 186649, 186651, 186653–186655, 186661, 186672, 186681, 186683, 186688, 186697–186699, 186703–186711, 186713, 186717, 186719, 186721–186723, 186728/188399, 186729/188400, 188370, 188371, 188374, 188375, 188384, 188387, 188388, 188392, 188394, 188397, 188404; Caura, AMNH 7567/5960, 7569/5962, 7572/5964, 7573/5965, 7574/5966, 7575/5967, 7578/5970, 7579/5971, 7581/5973, 7583/5975, 7584/5976, 7588/5979, 7589/5980, 7594/5985, 7596/5987, 7570/5988, 7598/5989; FMNH 5373, 5375; MCZ B7775, B7776; USNM 85570. **VENEZUELA (85): ARA-GUA:** Camp Rafael Rangel, 1260 m, USNM 317697–317699, 317702, 317707, 317708, 317712. **GUÁRICO:** 23 km NE of Calabozo, Hato Los Leones, Caño Agua Fría, 89 m, USNM 378822. **NUEVA ESPARTA:** 2 km N, 2 km E La Asunción, Cerro Matasiete, 405–420 m, EBRG 15081; USNM 405982; Cerro Copey, San Juan, 800 m, MHNLS 199. **SUCRE:** 4–5 km S, 24–25 km E Curúpano, near Manacal, 185–600 m, EBRG 15094; USNM 409826, 409829, 409831, 409839, 409842, 409843, 409848, 409851, 409852; 8 km N, 5 km E Güiría, Hacienda La Concordia, 7 m, USNM 409812; Latal, 3100 ft [945 m], AMNH 69698, 69704–69707, 69709–69712, 69715, 69717, 69720, 69722, 69723, 69725–69727, 69730, 69732–69735, 69737–69742, 69744–69749, 69751; Neverí, 2400 ft [732 m], AMNH 69651–69654, 69660–69662, 69664, 69665, 69671, 69673. **VARGAS (formerly DISTRITO FEDERAL):** Los canales de Naiguatá, Parque Nacional El Ávila, vertiente norte, 720 m, MHNLS 4865, 8531, 8574, 8587, 8596, 8627, 8645, 8648, 8650, 8668, 8673, 8675, 8686, 8690, 8715, 8716, 8726. Plus see Gazetteer (appendix 1) for 537 specimens from Colombia and western Venezuela.

***Heteromys australis* (total 20): COLOMBIA (1): VALLE DEL CAUCA:** Las Lomitas, 5000 ft [1524 m], AMNH 32240 (holotype of *Heteromys lomitensis*). **ECUADOR (4): ESMERALDAS:** San Javier [= San Javier de Cachaví], 60–120 ft [18–37 m], USNM 113304–13307 (topotypes of *Heteromys australis*). **PANAMA (15): DARIÉN:** Cana, 1800–2000 ft [549–610 m], USNM 178621, 178698, 178699 (holotype of *Heteromys australis consicus*), 178700, 179595; Amagal, 1000–2000 ft [305–610 m], ANSP 19491–19498,

19499 (holotype of *Heteromys australis pacificus*), 19779. Plus see Anderson (1999) for 271 additional specimens of *H. australis* from Colombia and Panama, Anderson and Jarrín-V. (2002) for 23 individuals from Ecuador, and Gazetteer (appendix 1) for lone specimen known from Venezuela.

***Heteromys desmarestianus* (species complex; total 64): COSTA RICA (11): CARTAGO:** Angostura, USNM 12903/38590, 12904/38591 (holotype of *Heteromys desmarestianus subaffinis*), 12905/36848; **SAN JOSÉ:** Escazú, 3000 ft [914 m], AMNH 131729 (holotype of *Heteromys desmarestianus underwoodi*); Escazú, Los Higuerones, AMNH 137299–137302; San Gerónimo Pirris, USNM 250348 (holotype of *Heteromys desmarestianus planifrons*), 250349, 256445. **MEXICO (10): CHIAPAS:** Chicharras, USNM 77516 (holotype of *Heteromys goldmani*), 77577, 77579–77582, 77694; **VERACRUZ:** Motzorongo, USNM 63718, 63719 (holotype of *Heteromys temporalis*), 63720. **PANAMA (43): COLÓN:** Río Indio, near Gatún, USNM 170919, 170920, 170975, 170976 (holotype of *Heteromys zonalis*); **CHIRIQUÍ:** Boquete, 4000–5800 ft [1219–1768 m], MCZ B10355, B10356 (holotype of *Heteromys repens*), B10358, B10360, B10361; Cerro Pando, ANSP 17835 (holotype of *Heteromys desmarestianus chiquiensis*), 17836, 17837, 18374–18377; **DARIÉN:** Mount Pirri, near head of Río Limón, 4500–5200 ft [1372–1585 m], USNM 178998–179004, 179006–179015, 179016 (holotype of *Heteromys crassirostris*), 179018–179020; **PANAMÁ:** Cerro Azul, 2500–3000 ft [762–914 m], USNM 171107 (holotype of *Heteromys panamensis*), 171108–171111, 171128. Plus see Anderson (1999) for additional specimens of *H. d. crassirostris* from Colombia and Panama.

***Heteromys gaumeri* (total 2): MEXICO (2): CAMPECHE:** Escarcega, 7 km N, 51 km E of, KU 93644; Escarcega, 103 km SE of, KU 93647.

***Heteromys nelsoni* (total 2): MEXICO (2): CHIAPAS:** Pinabete, USNM 77920 (holotype of *Heteromys nelsoni*), 77578.

***Heteromys oresterus* (total 9): COSTA RICA (9): SAN JOSÉ:** El Copey de Dota, 6000–6500 ft [1829–1981 m], UMMZ 64026, 64027 (holotype of *Heteromys oresterus*), 64028–64034.

***Heteromys teleus* (total 22): ECUADOR (22): GUAYAS:** Cerro Manglar Alto, eastern slope, AMNH 64675–64679; Cerro Manglar Alto, western slope, AMNH 64680–64693, 64694 (holotype of *Heteromys teleus*), 64695, 64696. Plus see Anderson and Jarrín-V. (2002) for 9 additional specimens from Ecuador.

APPENDIX 3

LISTS OF MEASURED SPECIMENS

Part A: Measured specimens in age class 4 from primary geographic samples. Abbreviated names used in the text appear in parentheses here. See appendices 1 and 2 for full provenience.

***Heteromys anomalus*: COLOMBIA: CESAR:** (Caracolicito) USNM 280214, 280215, 280224, 280229, 280242, 280243. **VENEZUELA: ARA-GUA:** (Rafael Rangel) USNM 317697–317699, 317702, 317707, 317708, 317712; **LARA:** (Yacambú) CVULA I-2728, 2732, 2736, 2742, 2743, 2750, 2754, 2755, 6162; EBRG 10302, 10612, 10616, 10618; MBUCV 4844, 4848, 4867; MCNUSB I-808, 809, 812, 813, 816, 852–855; **MÉRIDA:** (Cucuchica) CVULA I-5971, 5987, 5988, 5993, 6008, 6009, 6019; **SUCRE:** (Neverí) AMNH 69651–69654, 69660–69662, 69664, 69665, 69671, 69673; (Latal) AMNH 69705, 69710, 69711, 69726, 69732, 69733, 69739, 69742, 69744, 69748, 69751; (Manacal) EBRG 15094; USNM 409826, 409829, 409831, 409839, 409842, 409843, 409848, 409851, 409852; **TRU-JILLO:** (Valera) MBUCV 1824; EBRG 15050, 15058; USNM 371031, 371035, 372502, 372503, 372506; **VARGAS (formerly DISTRITO FEDERAL):** (Naiguatá) MHNLS 4865, 8531, 8574, 8587, 8596, 8627, 8645, 8648, 8650, 8668, 8673, 8675, 8686, 8690, 8715, 8716, 8726; **ZULIA:** (Tukuko) CVULA I-1890; MHNLS 7711, 7781, 7803, 7806, 7808; USNM 448546, 448547, 448556, 448558, 448559, 448561. **TRINIDAD AND TO-BAGO: TRINIDAD:** (Bush Bush Forest) AMNH 186626, 186627, 186631, 186633, 186634,

186636, 186639, 186641, 186643, 186649, 186651, 186653–186655, 186661, 186672, 186681, 186683, 186688, 186697–186699, 186703–186711, 186713, 186717, 186719, 186721–186723, 186728/188399, 186729/188400, 188370, 188371, 188374, 188375, 188384, 188387, 188388, 188392, 188394, 188397, 188404; (Caura) AMNH 7567/5960, 7575/5967, 7578/5970, 7588/5979, 7589/5980, 7594/5985.

***Heteromys oasicus*: VENEZUELA: FALCÓN:** (Paraguaná) EBRG 15110, 15111, 20697; USNM 456325.

Part B: Other measured specimens. See appendices 1 and 2 for full provenience.

***Heteromys anomalus*: COLOMBIA: CUNDI-NAMARCA:** ICN 1827–1829, 1832 1833, 1835, 1866; **LA GUAJIRA:** IND-M 5924; **MAGDALENA:** AMNH 15344, 15346–15348; 15350, 15351, 15353. **VENEZUELA: NUEVA ESPARTA:** EBRG 15081; MHNLS 199; USNM 405982; **SUCRE:** AMNH 69698, 69704, 69706, 69707, 69709, 69712, 69715, 69717, 69720, 69722, 69723, 69725, 69727, 69730, 69734, 69735, 69737, 68738, 69740, 69741, 69745–69747, 69749; **ZU-LIA:** FMNH 18622, 18623, 18625, 18626. **TRIN-IDAD AND TOBAGO: TRINIDAD:** AMNH 7569/5962, 7572/5964, 7573/5965, 7574/5966, 7579/5971, 7581/5973, 7583/5975, 7584/5976, 7596/5987, 7570/5988, 7598/5989, FMNH 5373, 5375; MCZ B7775, B7776; USNM 85570.

***Heteromys oasicus*: VENEZUELA: FALCÓN:** EBRG 15984, 20698; USNM 456324, 456327.

APPENDIX 4

DESCRIPTIVE STATISTICS

Sample size, mean \pm standard error, and range (minimum–maximum) are given for external measurements, mass, and cranial dimensions of adult specimens in age class 4 for the sample of *Heteromys oasicus* from the Peninsula de Paraguaná and for the 12 geographic samples of *Heteromys anomalus* (see appendices 1 and 2 for provenience and appendix 3 for museum catalog numbers). Linear measurements are in millimeters; mass in grams.

<i>Total length</i>				<i>Ear length (continued)</i>			
Paraguaná	4	236.5 \pm 4.87	227–250	Rafael Rangel	0	–	–
Caracolicito	6	301.7 \pm 1.76	296–308	Naiguatá	0	–	–
Tukuko	9	282.3 \pm 4.70	257–303	Neverí	0	–	–
Cucuchica	7	277.3 \pm 5.63	250–290	Latal	0	–	–
Valera	7	278.3 \pm 4.33	263–289	Manacal	10	18.5 \pm 0.34	17–20
Yacambú	24	293.7 \pm 2.99	262–323	Caura	6	18.8 \pm 0.54	17–20
Rafael Rangel	0	–	–	Bush Bush Forest	38	15.8 \pm 0.32	14–27
Naiguatá	1	286.0 \pm –	286–286	<i>Mass</i>			
Neverí	10	292.1 \pm 4.94	274–327	Paraguaná	4	43.8 \pm 2.69	38–51
Latal	11	293.2 \pm 2.91	279–312	Caracolicito	0	–	–
Manacal	10	282.2 \pm 4.83	258–302	Tukuko	9	73.0 \pm 4.57	58–100
Caura	6	282.3 \pm 3.51	274–298	Cucuchica	6	48.0 \pm 2.39	39–55
Bush Bush Forest	43	259.8 \pm 1.80	235–277	Valera	1	70.0 \pm –	70–70
<i>Tail length</i>				Yacambú	22	57.4 \pm 1.99	42–74
Paraguaná	4	118.5 \pm 1.19	115–120	Rafael Rangel	0	–	–
Caracolicito	6	164.5 \pm 2.28	157–171	Naiguatá	0	–	–
Tukuko	9	152.9 \pm 3.42	136–172	Neverí	0	–	–
Cucuchica	7	154.0 \pm 2.80	147–168	Latal	0	–	–
Valera	7	153.1 \pm 3.92	138–165	Manacal	10	60.1 \pm 3.86	49–87
Yacambú	24	162.5 \pm 2.21	140–180	Caura	0	–	–
Rafael Rangel	0	–	–	Bush Bush Forest	46	43.3 \pm 0.97	27–58
Naiguatá	1	152.0 \pm –	152–152	<i>Occipitonasal length</i>			
Neverí	10	163.5 \pm 2.23	155–180	Paraguaná	4	30.637 \pm 0.343	29.70–31.18
Latal	11	163.0 \pm 2.08	153–173	Caracolicito	6	36.123 \pm 0.395	35.04–37.46
Manacal	10	156.1 \pm 3.94	134–175	Tukuko	12	35.593 \pm 0.498	31.94–39.02
Caura	6	155.0 \pm 1.98	149–163	Cucuchica	7	34.633 \pm 0.254	33.72–35.57
Bush Bush Forest	43	142.0 \pm 1.31	120–155	Valera	8	35.039 \pm 0.413	33.22–36.74
<i>Hind foot length</i>				Yacambú	25	34.645 \pm 0.216	32.13–35.90
Paraguaná	4	29.0 \pm 0.41	28–30	Rafael Rangel	7	36.601 \pm 0.475	34.98–38.29
Caracolicito	6	33.8 \pm 0.31	33–35	Naiguatá	17	34.837 \pm 0.432	31.06–38.36
Tukuko	9	34.3 \pm 0.41	33–36	Neverí	11	36.345 \pm 0.361	34.89–38.85
Cucuchica	7	36.1 \pm 1.64	31–45	Latal	11	36.530 \pm 0.251	35.15–37.90
Valera	8	34.3 \pm 0.70	32–38	Manacal	10	35.190 \pm 0.464	32.85–38.04
Yacambú	24	33.9 \pm 0.32	32–37	Caura	6	35.248 \pm 0.352	34.05–36.27
Rafael Rangel	0	–	–	Bush Bush Forest	50	33.353 \pm 0.144	31.47–35.57
Naiguatá	1	31.0 \pm –	31–31	<i>Zygomatic breadth</i>			
Neverí	11	35.4 \pm 0.36	33–37	Paraguaná	4	14.322 \pm 0.147	14.01–14.72
Latal	11	35.9 \pm 0.32	34–37	Caracolicito	6	16.183 \pm 0.250	15.42–16.97
Manacal	10	35.3 \pm 0.50	33–38	Tukuko	12	16.553 \pm 0.231	15.12–17.90
Caura	6	35.2 \pm 0.31	34–36	Cucuchica	7	16.043 \pm 0.143	15.47–16.45
Bush Bush Forest	38	32.8 \pm 0.23	28–35	Valera	8	16.238 \pm 0.261	15.09–17.54
<i>Ear length</i>				Yacambú	25	16.165 \pm 0.114	14.64–16.87
Paraguaná	4	17.3 \pm 0.75	15–18	Rafael Rangel	7	17.060 \pm 0.369	15.80–18.23
Caracolicito	6	19.0 \pm 0.26	18–20	Naiguatá	17	15.757 \pm 0.164	14.42–16.80
Tukuko	9	17.3 \pm 0.33	15–18	Neverí	11	16.675 \pm 0.167	15.93–17.61
Cucuchica	7	20.4 \pm 1.43	16–27	Latal	11	16.223 \pm 0.154	15.46–16.89
Valera	8	17.8 \pm 0.37	16–19	Manacal	10	16.015 \pm 0.177	14.90–16.95
Yacambú	24	19.7 \pm 0.64	17–29	Caura	6	16.058 \pm 0.127	15.69–16.51
				Bush Bush Forest	50	15.459 \pm 0.073	14.42–16.95

APPENDIX 4

(Continued)

<i>Rostral length</i>				<i>Maxillary tooththrow length</i>			
Paraguana	4	12.983 ± 0.187	12.45–13.29	Paraguana	4	4.620 ± 0.092	4.39–4.82
Caracolicito	6	16.303 ± 0.229	15.64–16.97	Caracolicito	6	5.188 ± 0.087	4.92–5.49
Tukuko	12	15.508 ± 0.227	13.94–17.01	Tukuko	12	5.421 ± 0.071	4.87–5.80
Cucuchica	7	15.286 ± 0.114	14.96–15.76	Cucuchica	7	5.257 ± 0.042	5.04–5.35
Valera	8	15.336 ± 0.209	14.33–15.89	Valera	8	5.419 ± 0.096	5.04–5.88
Yacambú	25	15.401 ± 0.127	13.69–16.25	Yacambú	25	5.458 ± 0.048	4.88–6.05
Rafael Rangel	7	16.284 ± 0.273	15.43–17.28	Rafael Rangel	7	5.450 ± 0.121	4.83–5.77
Naiguatá	17	15.409 ± 0.192	13.60–16.63	Naiguatá	17	5.132 ± 0.051	4.67–5.45
Neverí	11	16.285 ± 0.207	15.39–17.60	Neverí	11	5.516 ± 0.060	5.26–5.83
Latal	11	16.315 ± 0.160	15.38–16.97	Latal	11	5.469 ± 0.053	5.17–5.76
Manacal	10	15.381 ± 0.235	14.48–17.00	Manacal	10	5.213 ± 0.094	4.80–5.67
Caura	6	15.598 ± 0.236	14.55–16.15	Caura	6	5.353 ± 0.050	5.20–5.50
Bush Bush Forest	50	14.641 ± 0.078	13.47–16.13	Bush Bush Forest	50	5.115 ± 0.023	4.77–5.70
<i>Nasal length</i>				<i>Interparietal width</i>			
Paraguana	4	11.893 ± 0.135	11.54–12.11	Paraguana	4	8.007 ± 0.241	7.42–8.45
Caracolicito	6	15.438 ± 0.191	14.66–16.01	Caracolicito	6	9.067 ± 0.187	8.54–9.69
Tukuko	12	14.287 ± 0.244	12.74–16.10	Tukuko	12	9.595 ± 0.131	8.85–10.30
Cucuchica	7	13.939 ± 0.121	13.65–14.53	Cucuchica	7	9.293 ± 0.018	9.20–9.34
Valera	8	14.083 ± 0.265	12.99–15.21	Valera	8	9.060 ± 0.224	7.90–9.95
Yacambú	25	14.092 ± 0.138	12.34–15.47	Yacambú	25	8.598 ± 0.106	7.56–9.79
Rafael Rangel	7	14.747 ± 0.322	13.75–15.98	Rafael Rangel	7	9.149 ± 0.271	8.27–10.01
Naiguatá	17	13.960 ± 0.215	11.93–15.35	Naiguatá	17	8.669 ± 0.166	7.06–9.93
Neverí	11	14.595 ± 0.215	13.79–16.04	Neverí	11	8.705 ± 0.121	8.02–9.11
Latal	11	14.809 ± 0.142	14.11–15.51	Latal	11	8.450 ± 0.104	7.94–8.97
Manacal	10	13.997 ± 0.232	12.65–15.32	Manacal	10	8.504 ± 0.140	7.70–9.33
Caura	6	14.187 ± 0.234	13.32–14.76	Caura	6	8.500 ± 0.109	8.03–8.76
Bush Bush Forest	50	13.275 ± 0.078	11.92–14.44	Bush Bush Forest	50	7.979 ± 0.053	7.28–8.78
<i>Least interorbital constriction</i>				<i>Interparietal length</i>			
Paraguana	4	7.318 ± 0.046	7.25–7.45	Paraguana	4	4.435 ± 0.102	4.17–4.66
Caracolicito	6	8.277 ± 0.154	7.76–8.81	Caracolicito	6	4.900 ± 0.089	4.62–5.27
Tukuko	12	8.681 ± 0.139	8.10–9.78	Tukuko	12	5.216 ± 0.100	4.64–5.67
Cucuchica	7	8.160 ± 0.056	7.97–8.40	Cucuchica	7	5.061 ± 0.210	4.51–5.89
Valera	8	7.911 ± 0.158	7.25–8.50	Valera	8	4.749 ± 0.089	4.18–4.98
Yacambú	25	8.352 ± 0.050	7.82–8.78	Yacambú	25	4.773 ± 0.071	4.03–5.51
Rafael Rangel	7	8.533 ± 0.209	7.79–9.37	Rafael Rangel	7	4.731 ± 0.133	4.16–5.16
Naiguatá	17	8.308 ± 0.081	7.81–8.87	Naiguatá	17	4.856 ± 0.112	4.09–5.63
Neverí	11	8.380 ± 0.109	7.89–9.00	Neverí	11	5.378 ± 0.063	5.13–5.83
Latal	11	8.534 ± 0.080	8.18–9.07	Latal	11	5.112 ± 0.055	4.86–5.39
Manacal	10	7.999 ± 0.095	7.66–8.60	Manacal	10	5.266 ± 0.140	4.37–5.73
Caura	6	8.428 ± 0.038	8.25–8.51	Caura	6	5.138 ± 0.135	4.69–5.48
Bush Bush Forest	50	7.826 ± 0.040	7.28–8.59	Bush Bush Forest	50	4.918 ± 0.042	4.14–5.48
<i>Squamosal breadth</i>				<i>Parietal breadth</i>			
Paraguana	4	13.612 ± 0.123	13.39–13.94	Paraguana	4	11.567 ± 0.087	11.40–11.81
Caracolicito	6	14.815 ± 0.078	14.53–15.03	Caracolicito	6	12.618 ± 0.076	12.30–12.81
Tukuko	12	15.260 ± 0.140	14.13–16.00	Tukuko	12	12.853 ± 0.145	12.29–13.94
Cucuchica	7	15.123 ± 0.127	14.72–15.63	Cucuchica	7	12.714 ± 0.092	12.43–13.00
Valera	8	14.999 ± 0.177	13.91–15.51	Valera	8	12.572 ± 0.197	11.34–13.05
Yacambú	25	14.693 ± 0.135	12.25–15.81	Yacambú	25	12.531 ± 0.073	11.72–13.29
Rafael Rangel	7	15.651 ± 0.132	15.12–15.98	Rafael Rangel	7	12.720 ± 0.155	12.19–13.35
Naiguatá	17	15.016 ± 0.112	14.09–15.69	Naiguatá	17	12.342 ± 0.080	11.67–13.15
Neverí	11	15.081 ± 0.096	14.65–15.74	Neverí	11	12.614 ± 0.097	12.10–13.11
Latal	11	15.161 ± 0.090	14.46–15.50	Latal	11	12.726 ± 0.097	11.97–13.05
Manacal	10	14.777 ± 0.127	14.21–15.45	Manacal	10	12.236 ± 0.057	11.97–12.47
Caura	6	14.642 ± 0.114	14.19–14.89	Caura	6	12.268 ± 0.120	11.80–12.55
Bush Bush Forest	50	14.224 ± 0.043	13.65–14.85	Bush Bush Forest	50	11.924 ± 0.048	10.55–12.85

APPENDIX 4
(Continued)

<i>Skull depth</i>			
Paraguaná	4	9.895 ± 0.100	9.71–10.16
Caracolicito	6	10.722 ± 0.041	10.61–10.84
Tukuko	12	11.079 ± 0.103	10.35–11.65
Cucuchica	7	10.960 ± 0.073	10.78–11.37
Valera	8	10.819 ± 0.174	9.84–11.39
Yacambú	25	10.986 ± 0.056	10.50–11.57
Rafael Rangel	7	11.416 ± 0.103	11.04–11.67
Naiguatá	17	11.007 ± 0.074	10.45–11.62
Neverí	11	11.159 ± 0.061	10.79–11.42
Latal	11	11.135 ± 0.079	10.52–11.48
Manacal	10	10.718 ± 0.101	10.36–11.40
Caura	6	10.877 ± 0.097	10.66–11.34
Bush Bush Forest	50	10.483 ± 0.048	9.77–12.00