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PRELIMINARY REVIEW OF THE SYSTEMATICS AND BIOGEOGRAPHY OF THE SPINY POCKET MICE (*HETEROMYS*) OF COLOMBIA

por

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Resumen

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Por medio del estudio de especímenes de museo, se confirma la presencia en Colombia de tres especies de ratones de abazones del género *Heteromys*. *Heteromys anomalus* habita los bosques y zonas de cultivos de la costa caribeña y del alto Río Magdalena y su distribución se extiende al oriente en Venezuela. *Heteromys australis* se distribuye en los bosques húmedos de tierras bajas del Chocó en el oriente de Panamá, el occidente de Colombia y el noroccidente del Ecuador. Asimismo, habita áreas de bosques montanos húmedos en las tres corilleras andinas colombianas y en Venezuela existe una población periférica que habita parte de la Cordillera de Mérida. Se confirma la presencia de una especie del complejo *Heteromys desmarestianus* para Suramérica, con base en una localidad al extremo del noroccidente colombiano, referida como *H. desmarestianus crassirostris*. Se revisa la taxonomía de las especies colombianas y se exponen e ilustran caracteres diagnósticos. Los patrones de distribución de las especies sugieren que los heterómino colonizaron a Suramérica en una etapa más temprana de lo que se pensaba anteriormente. El presente trabajo propone varias hipótesis biogeográficas que deben ser probadas en estudios futuros. Se resalta la necesidad de llevar a cabo revisiones taxonómicas y de verificar las identificaciones de ejemplares de museo, en estudios de biodiversidad y evolución.

Palabras clave: *Heteromys*, Morfología, Sistemática, Biogeografía, Colombia, Intercambio de fauna, Suramérica,

Abstract

Study of museum specimens confirms the presence of three species of spiny pocket mice (*Heteromys*) in Colombia. *Heteromys anomalus* inhabits forests and agricultural areas along

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the Caribbean coast, as well as similar habitats in the upper Río Magdalena. Its distribution continues eastward into Venezuela. *Heteromys australis* is distributed in wet lowland rainforest in the Chocó of eastern Panama, western Colombia, and northwestern Ecuador and continues its distribution in montane rainforests of the Andes in the Cordillera Occidental, the Cordillera Central, and the Cordillera Oriental of Colombia. A disjunct population inhabits part of the Cordillera de Mérida in Venezuela. A species of the *Heteromys desmarestianus* complex, here referred to as *H. desmarestianus crassirostris,* is confirmed for one South American locality in extreme northwestern Colombia. The taxonomy of these species is reviewed, and diagnostic characters are provided and illustrated. The complicated and disjunct distributions of these species suggest that heteromyines colonized South America earlier than previously thought. This article raises several biogeographic questions to be tested in future studies and emphasizes the need for systematic revisions and the verification of museum holdings for studies of biodiversity and evolution.

Key words: *Heteromys*, Morphology, Systematics, Biogeography, Colombia, Faunal interchange, South America.

Introduction

Colombia holds a pivotal geographic position at the northwestern corner of South America, where the Isthmus of Panama joins Central America to the geologically and faunistically distinct South America (Fig. 1). Furthermore, in southern Colombia, the Andes split into three major ranges (the Cordillera Occidental, the Cordillera Central, and the Cordillera Oriental) separated by two low, dry valleys, those of the Río Cauca and the Río Magdalena. Thus, Colombia possesses a complicated and varied topography and a biota with concomitantly complicated distributional patterns.

Small rodents in northwestern South America

Rodents represent an opportune group for studies of historical biogeography and patterns of diversity. Small rodents are diverse in Colombia, with at least 35 native genera (of Echimyidae, Heteromyidae, and Sigmodontinae) present **Rodríguez-Mahecha *et al.*** (1995). The low dispersal ability of non-volant mammals has contributed to their speciation, producing many sets of related species distributed allopatrically throughout Colombia and adjacent countries. Furthermore, these rodents show great ecological diversification. Elevation and rainfall seem to explain the broadest distributional patterns of most species. The great majority could be categorized as animals of either wet lowlands, dry lowlands, or wet highlands. Few dry highland areas are present in the country, and they are not noteworthy as areas of endemism. In addition to these broad categories, however, most genera have particular habitat requirements, such as streams (ichthyomyines and *Nectomys*), trees (*Oecomys, Rhipidomys,* and many echimyids), or grassy areas (*Akodon* and *Sigmodon*), further contributing to the diversity of local communities.

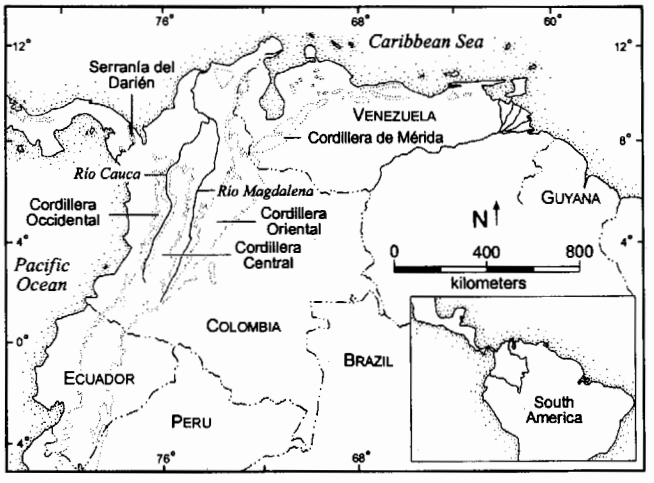

Figure 1. Map of Colombia and surrounding areas. Note the location of the Río Cauca and the Río Magdalena, as well as the various cordilleras of the Andes.

Given recent advances and syntheses in comparative biology, **Brooks & McLennan** (1991), **Ricklefs & Schluter** (1993), community ecology, **Brown** (1995), **Rosenzweig** (1995), and molecular genetics **Avise** (1994), conditions are ripe for distributional and comparative studies of rodents in northwestern South America. Such meta-analyses depend on solid alpha-systematics, however, and presently not all genera of rodents can be identified satisfactorily to species. Recently, several authors have advanced the systematic knowledge of some groups (*e.g.*, **Carleton & Musser** (1989), **Gómez-Laverde *et al.*** (1997), **Musser *et al.*** (1998), **Voss** (1988, 1991, 1992), but most genera lack careful systematic revisions. This paper initiates the process for the spiny pocket mice (*Heteromys*) of Colombia and contiguous regions of surrounding

countries. Future papers will complete the revision of this group for other geographic regions.

The forest spiny pocket mice, *Heteromys*

Spiny pocket mice of the genus *Heteromys* belong to the family Heteromyidae, which originated in North America **Rogers** (1990). In the key to the genus provided by **Schmit *et al.*** (1989), couplets 4 and 5 often fail to correctly identify individuals of these species. The descriptions of *Heteromys anomalus* and *H. australis* are inadequate in **Eisenberg** (1989, 1999), and the distribution of neither is mapped in Colombia. *Heteromys* is the only genus of the family to have colonized South America, where three species are thought to occur, **Williams *et al.*** (1993), although further research undoubtedly will uncover others. Spiny pocket mice are terrestrial granivores found primarily in forest habitats, **Sánchez-Cordero & Fleming** (1993). They are relatively common in museum collections, but their conservative external and cranial morphology and marked age variation have long hindered conclusive taxonomic revisions.

Emmons (1997:197), **Hall** (1981:597), **Patton** (1993:481), **Reid** (1997:199), and **Williams *et al.*** (1993:100–104) each expressed the need for continued systematic revision of the group, especially regarding the southern species. Recent advances in statistical techniques provide for the removal of age variation in morphometric data sets, **Anderson** (unpublished data), **Burnaby** (1966), **Rohlf & Bookstein** (1987). Combined with genetic research **Rogers** (1990), these techniques have allowed for a reevaluation of the taxonomy and distributions of southern members of the genus *Heteromys* **Anderson & Soriano,** (1999); **Anderson** (unpublished data); **Anderson & Rogers** (unpublished data), leading to the present review of the species of *Heteromys* in Colombia.

Biogeographic questions

Based on the lack of a fossil history for the group in South America, **Marshall *et al.*** (1982) considered that heteromyids had entered the southern continent during the Holocene—that is, after the end of the last Ice Age (ca. 10,000 B.P). **Anderson & Soriano** (1999), however, reported a disjunct population of *Heteromys australis* in the Mérida Andes of Venezuela, suggesting that rather than colonizing South America during the Holocene, *H. australis* had actually undergone a range retraction concomitant with warmer, drier climates in the past 10,000 years. A detailed picture of the distributional patterns of heteromyids in South America could resolve many debates concerning their history.

Methods and Materials

Museum specimens

I examined specimens of *Heteromys* from Colombia and adjacent countries in the collections of thirteen natural history museums (Appendix 1). In addition to elucidating diagnostic characters for each species, I recorded the original identification and complete locality information for each specimen. Specimens were assigned age classes based on patterns of tooth wear and molt following **Rogers & Schmidly** (1982). I took cranial measurements in mm as defined by **Rogers & Schmidly** (1982), and copied external measurements from specimen tags. Descriptive statistics were calculated for adults of age classes 4 and 5 for one series of each species (Appendix 2) using **MINITAB** (1996). Multivariate morphometric analyses will be published elsewhere. All cranial drawings are based on original camera lucida tracings of mature adult female specimens in age class four.

Specimens were examined from the following museum collections (abbreviations follow **Hafner *et al.*** (1997), when available; asterisks (*) denote collections with material from Colombia): Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History, New York (AMNH*); Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); Field Museum, Chicago (FMNH*); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN*); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, IAvH—includes the former INDERENA collection—Villa de Leiva, Boyacá (IND-M*); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museo del Instituto La Salle, Bogotá (MLS*); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ*); United States National Museum of Natural History, Washington, DC (USNM*); Universidad del Valle, Cali (UV*); University of Kansas Natural History Museum, Lawrence (KU); and University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

Geographic coordinates

Geographic coordinates of latitude and longitude (Appendix 1) came from a variety of sources, in the following order of precedence. Some collectors noted coordinates directly on the specimen tags or in subsequent publications (*e.g.*, **Alberico** (1983), **Hershkovitz** (1947, 1977). Because early workers commonly collected both birds and mammals, the *Ornithological Gazetteer of Colombia* **Paynter** (1997) provides latitude and longitude for most specimens of *Heteromys* collected at the end of the 19th century and the beginning of the 20th century. I used recent

maps of each Colombian department produced by the Instituto Geográfico Agustín Codazzi, Bogotá (IGAC) to locate more recent collection localities and assign approximate coordinates. Recent revisions of other rodents (*e.g.*, **Musser *et al.***, 1998) sometimes provided latitude and longitude for additional localities. Appendix 1 gives latitude and longitude for all localities for which coordinates could be satisfactorily determined. Although I took no coordinates from **IGAC** (1996), the use of this notable reference often proved indispensable in conjunction with the IGAC maps.

Results

Examination of museum collections confirmed the presence of three species of *Heteromys* in Colombia. I here give their known distributions, review taxonomic issues, provide and illustrate diagnostic morphological characters, and summarize available data on the natural history of each species. In addition to these three species, a species that is morphologically similar to *H. australis* may be present in Antioquia (see taxonomic review of *H. australis*).

Comments on identifying spiny pocket mice

Like many rodents, spiny pocket mice exhibit indeterminate growth, in which individuals continue to grow well past sexual maturity. Furthermore, an individual's skull changes shape as it grows, according to parameters of allometric growth. This marked age variation, coupled with sexual dimorphism in size and shape, produces vast morphological variation within a single population. Such intrapopulational variation makes species identification difficult, and specimens should be compared with confirmed voucher specimens of the same semaphoront (same age class and gender, in this case) to attain a valid identification. Juveniles of all species have soft, gray pelage and are extremely difficult to identify. Thus, large series of males and females of all ages are needed in musuem collections. Without such series, the present review would have been impossible.

Two factors, fortunately, aid in the identification of spiny pocket mice. First, patterns of tooth wear and molt allow for objective relative aging of specimens. Standard age categories for the genus are provided in **Rogers & Schmidly** (1982). In *Heteromys desmarestianus crassirostris,* however, the scheme is slightly offset, as the molars are often worn to the "u"-shape of age class 4 before the permanent premolars are fully erupted. Such individuals are usually still in juvenile pelage and should be classified as age class 2, based on the juvenile pelage and presence of the deciduous premolars.

Secondly, the geographic ranges of species of *Heteromys* do not overlap widely. Where species' ranges do come together, they are usually segregated by habitat type (*c.f.*, **Rogers & Engstrom**, 1992, for two species of the related genus *Liomys*). Indeed, among all the museum collections consulted, I found only one locality of sympatry in Colombia (Córdoba: Socorré, upper Río Sinú), but the field notes of the collector, Philip Hershkovitz, did not indicate whether the two species were collected in the same habitats. Although geography aids in identification, zones of contact between species probably exist in several areas of the country. Hence, preserved voucher specimens, especially well-cleaned cranial material, are critical for identification by comparison with previously confirmed specimens and consultation of the diagnoses and figures provided here.

Species Accounts

Heteromys anomalus (Thompson, 1815) Caribbean spiny pocket mouse

Heteromys anomalus is a large, robust pocket mouse with grizzled brown dorsal pelage. Its tail is strongly bicolored and usually longer than the head-and-body length (Table 1). This species has stiff spines throughout its range in Colombia and displays minimal geographic variation in external characters. One notable exception is the population at Antioquia: Urabá, Río Currulao, which is much darker than other coastal *H. anomalus.* The ears of *H. anomalus* are large, pale, and rounded, distinctive when compared with any other species of *Heteromys.*

Cranially, *Heteromys anomalus* is remarkable for its large, elongated, robust skull (Table 1, Fig. 2). The ante-

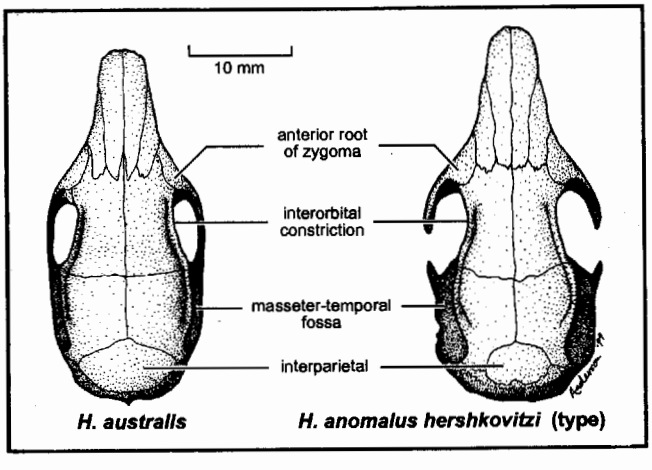

Figure 2. Dorsal views of the crania of *Heteromys australis* (*left,* UV 5928, Valle: Bajo Calima) and *H. anomalus* (*right,* ICN 1832—holotype of *Heteromys anomalus hershkovitzi,* Cundinamarca: Caparrapí, Volcanes). Both specimens are adult females in age class 4 **Rogers & Schmidly** (1982).

rior (maxillary) roots of the zygoma are wide and strong. The rostrum is wide, but the interorbital constriction is narrow. The masseter-temporal fossae ("masseteric fossae" in **Anderson & Soriano** (1999) are characteristically deep and well excavated.

Comparisons.—*Heteromys anomalus* is the largest pocket mouse in Colombia (Table 1). It dwarfs *H. d. crassirostris* and is decidedly larger than *H. australis*. Its pale, hispid dorsal coloration separates it from the slaty gray *H. australis* and the dark chocolate brown *H. d.*

Table 1. External and cranial measurements (mm) for adult *Heteromys* of age classes 4 and 5 **Rogers & Schmidy** (1986) from selected localites in Colombia and Panama. See Appendix 2 for exact localities and specimen numbers. Statistics are given as mean ± one standar error, sample size, and (minimum - maximum)

	H. anomalus Cesar: Caracolicito (Colombia)	*H. australis* Antioquia: Valdivia (Colombia)	*H. d. crassirostris* Darién: Mali Camp (Panamá)
Total length	294.9 ± 3.32, 26 (260.0–331.0)	278.3 ± 3.67, 12 (252.0–299.0)	266.8 ± 2.26, 32 (243.0–294.0)
Head-and-body length	133.3 ± 1.73, 26 (110.0–147.0)	129.1 ± 2.35, 12 (119.0–145.0)	127.55 ± 1.02, 33 (117.0–138.0)
Tail length	161.7 ± 2.37, 26 (137.0–184.0)	149.3 ± 2.12, 12 (133.0–160.0)	139.4 ± 1.75, 32 (120.0–157.0)
Tail/head-and-body ratio (%)	121.7 ± 2.03, 26 (94.5–143.7)	115.9 ± 2.11, 12 (102.1–126.0)	109.5 ± 1.44, 32 (93.5–124.0)
Hind foot length	34.5 ± 0.42, 26 (31.0–42.0)	33.5 ± 0.34, 12 (31.0–35.0)	32.0 ± 0.17, 33 (29.0–34.0)
Ear length	19.2 ± 0.15, 26 (18.0–21.0)	15.9 ± 0.23, 10 (15.0–17.0)	17.1 ± 0.12, 31 (16.0–19.0)
Greatest skull length	36.7 ± 0.30, 12 (35.0–38.1)	35.0 ± 0.24, 10 (33.3–35.8)	33.5 ± 0.15, 31 (32.2–35.1)
Zygomatic breadth	16.5 ± 0.19, 11 (15.4–17.3)	16.3 ± 0.11, 11 (15.6–16.9)	15.6 ± 0.07, 31 (14.6–16.2)
Rostral length	16.6 ± 0.16, 12 (15.6–17.3)	15.7 ± 0.09, 11 (15.0–16.1)	15.0 ± 0.10, 34 (13.3–16.1)
Nasal length	15.6 ± 0.16, 12 (14.7–16.5)	14.4 ± 0.13, 11 (13.7–15.0)	13.5 ± 0.09, 34 (12.0–14.3)
Least interorbital constriction	8.4 ± 0.10, 12 (7.8–8.9)	8.1 ± 0.07, 12 (7.7–8.5)	8.9 ± 0.05, 33 (8.2–9.7)
Mastoid breadth	14.8 ± 0.07, 12 (14.5–15.1)	15.0 ± 0.07, 9 (14.7–15.3)	14.7 ± 0.06, 32 (14.0–15.3)
Maxillary toothrow length	5.3 ± 0.10, 12 (4.9–6.2)	5.3 ± 0.06, 12 (4.9–5.6)	4.9 ± 0.04, 34 (4.6–5.4)
Interparietal width	9.3 ± 0.13, 12 (8.5–10.1)	10.1 ± 0.09, 9 (9.6–10.4)	8.9 ± 0.08, 33 (8.1–10.0)
Interparietal length	4.9 ± 0.10, 11 (4.20–5.30)	5.9 ± 0.15, 10 (4.9–6.6)	4.9 ± 0.06, 32 (4.0–5.6)
Skull depth	10.7 ± 0.04, 10 (10.5–10.9)	11.0 ± 0.05, 10 (10.7–11.3)	10.6 ± 0.04, 31 (10.1–11.0)

crassirostris. Juveniles of *H. anomalus* are paler than juvenile *H. australis*. Its tail is much longer than those of other Colombian species (and almost always longer than head-and-body length) and is characteristically bicolored. Its distinctively rounded ears are much larger and paler than in *H. australis* or *H. d. crassirostris*.

Cranially, *Heteromys anomalus* is larger, more elongated, and more robust than either *H. australis* or *H. d. crassirostris*, so much so that no further comparisons with *H. d. crassirostris* need be made (Table 1). Compared with *H. australis* (Fig. 2), *H. anomalus* has more robust zygomatic arches, well excavated masseter-temporal fossae, and an elongated, strongly ridged braincase, in contrast to the wider, inflated braincase of *H. australis*. The zygomatic arches are complete in adults of all species of *Heteromys*; those of many specimens are broken (Fig. 2).

Taxonomic review.—Two forms named from Colombia are conspecific with *Heteromys anomalus* **Thompson** (1815): *Heteromys jesupi* J. A. Allen, 1899 (from the lower northwestern slopes of the Sierra Nevada de Santa Marta), and *Heteromys anomalus hershkovitzi* Hernández-Camacho, 1956 (from the western foothills of the Cordillera Oriental). Specimens of the type series of *H. jesupi* are nearly indistinguishable from other populations of *H. anomalus* in northern Colombia and clearly intergrade with specimens of *H. anomalus* from the Caribbean coast of Venezuela and the Serranía de Perijá on the Colombo-Venezuelan border. Although *H. anomalus* was named based on material from Trinidad, the mainland populations differ only moderately from that insular population. *Heteromys anomalus hershkovitzi* is slightly differentiated from the coastal populations and probably has a disjunct range, but does not represent a separate evolutionary species.

Notes on the type locality of *Heteromys anomalus* Hershkovitzi.—**Hernández-Camacho** (1956:3) gave the type locality for *Heteromys a. hershkovitzi* as "Volcanes, cerca a la cabecera del corregimiento de Córdoba, Municpio de Caparrapí, Departamento de Cundinamarca; vertiente occidental de la Cordillera Oriental. Colombia. Alt. 250 metros." He added the following footnote (**Hernández-Camacho,** 1956:3), "Según informes recibidos, Volcanes se halla situado muy cerca a la Hacienda de "Tatí", que aparece indicada al noreste de Caparrapí en el mapa oficial del Departamento de Cundinamarca, tercera edición, Bogotá; 1941. Las coordenadas geográficas de dicha hacienda son aproximadamente: long. 74° 34' W de Greenwich, lat. 5° 26' 20" N."

More detailed, modern maps allow for a more precise localization of Volcanes. *Tatí* appears on the 1941 map of Cundinamarca (OL, 1941), but it is situated northwest, not northeast, of Caparrapí. *Tatí* also is found on more detailed recent maps of Cundinamarca (IGAC, 1973, 1976), as is *Volcanes*, which is not present on the 1941 map. In IGAC (1973), *Volcanes* is a place name situated ca. 12 km NNW of Caparrapí and ca. 7 km NNE of Córdoba, at ca. 5° 27' N, 74° 31' W. *Tatí* (IGAC, 1973) is located ca. 15 km NNW of Caparrapí and ca. 8 km N of Córdoba, at ca. 5° 28' N, 74° 33' W. *Volcanes* lies at ca. 1000 m, near the headwaters of the Quebrada Carbonera, a western-draining affluent of the Quebrada Pita (IGAC, 1976). *Tatí* is situated west of the Quebrada Pita at almost 1000 m (IGAC, 1976). If the elevation (250 m) given by **Hernández-Camacho** (1956) is correct, the type locality of *H. a. hershkovitzi* probably lies closer to the town of Córdoba, which is located lower, on the Río Negrito. None of the specimen tags I examined from the type series bore elevations, however; thus, alternatively the type may have been collected very near Volcanes, at ca. 1000 m. Other small mammals have been reported from Volcanes, such as *Zygodontomys brunneus* **Voss,** (1992) and *Oryzomys*

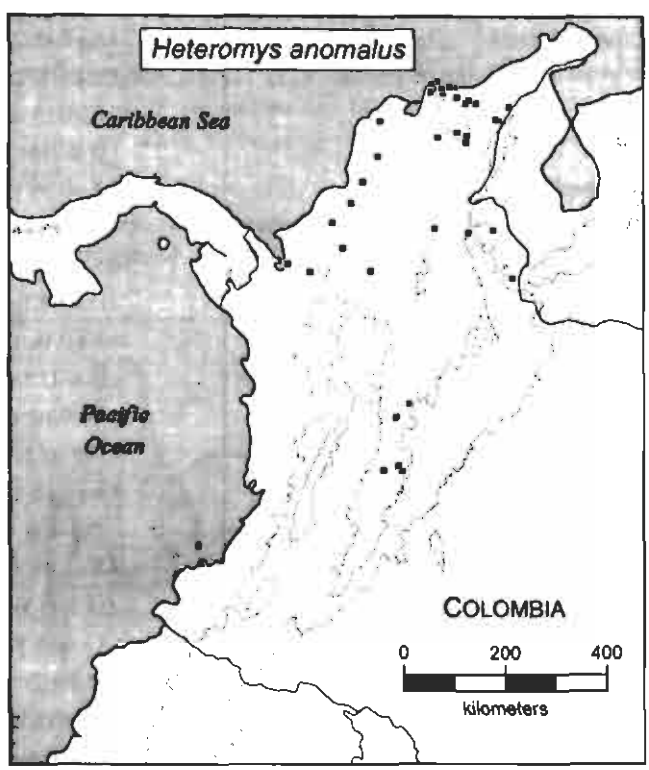

Figure 3. Map showing collection localities of *Heteromys anomalus* in Colombia (squares). *H. anomalus* continues its distribution to the east in Venezuela and Trinidad & Tobago. Only georeferenced localities are shown here; see Appendix 1 for exact collection localities for all specimens examined.

talamancae (Musser *et al.*, 1998). These species are known from other nearby localities slightly above 1000 m, as well as at the base of the Río Magdalena valley, consistent with either hypothesis.

Known distribution.—***Heteromys anomalus*** (Fig. 3) ranges along the northern (Caribbean) coast of Colombia in a wide variety of habitats, but especially in dry (deciduous) seasonal forests and agricultural areas, although it is found in wet forests on the northern side of the Sierra Nevada de Santa Marta. An apparently disjunct population inhabits the Río Magdalena valley in similar habitats. The coastal population extends into Venezuela and Trinidad & Tobago in the east—where it is found in both wet and dry areas (**Anderson & Soriano** (1999)—but does not enter Panama (*contra* **Méndez** (1993), **Nowak** (1999), **Rogers** (1990), **Williams *et al.*** (1993). The specimen reported by **Rogers** (1990) from 1200 m on Cerro Pirre actually represents *H. australis*. Specimens reported as *H. anomalus* by **Alberico** (1983) from Valle del Cauca also are *H. australis*. In Colombia, *H. anomalus* is found primarily at low elevations, but occasionally extends up the lower skirts of certain mountain ranges, such as the Sierra Nevada de Santa Marta and the Serranía de Perijá, to around 1500 meters.

Natural history.—Philip Hershkovitz (*in litt.*, June 1996) wrote that at Bolívar: San Juan Nepumuceno, *Heteromys anomalus* was "equally common in open fields, pastures, and second growth woodland. Nests in all situations." His field notes indicate that at Cesar: Colonia Agrícola de Caracolicito, it was found in "platanales, yucales, cañales, potreros, houses, along streams (very common), rice and corn fields, and forest," but that it was most abundant in areas near human settlement. At Córdoba: Catival, upper Río San Jorge, Hershkovitz stated that *H. anomalus* was "the most abundantly taken species here. The habit of this mouse of eating its fill and then filling its cheek pouches with food for storing elsewhere may explain the relative abundance of the animal" (in contrast to sigmodontine rodents, which generally do not cache food). The cheek pouches can each be stuffed to twice the size of the animal's head (**Hershkovitz, *in litt.***, June 1996). More recently, **Adler *et al.*** (1997) encountered *H. anomalus* at low, fluctuating densities in a similar agricultural setting.

Heteromys australis Thomas, 1901 Southern spiny pocket mouse

Heteromys australis is a small pocket mouse with dark, slaty gray dorsal pelage. Its tail tends to be only slightly longer than head-and-body length (Table 1), and varies from uniformly dark to fairly bicolored (dark dorsally, white ventrally). Specimens from the Pacific lowlands near Buenaventura (Valle del Cauca) reach the maximal melanistic condition found in the species, whereas specimens from other lowland areas and all highland localities tend to have more bicolored tails. This species also varies clinally in the spininess of its dorsal pelage: specimens from lowland areas are quite stiff, but at higher elevations, the fur is softer. Such intraspecific variation in pelage stiffness also occurs in at least three other species of *Heteromys* (Anderson, unpublished data). This variation may represent an adaptive interplay between shedding water off the fur in the lowlands (spiny pelage) versus the greater insulatory properties (of softer, more woolly pelage) in the highlands.

Cranially, *Heteromys australis* is moderately robust for a spiny pocket mouse and of intermediate size (Table

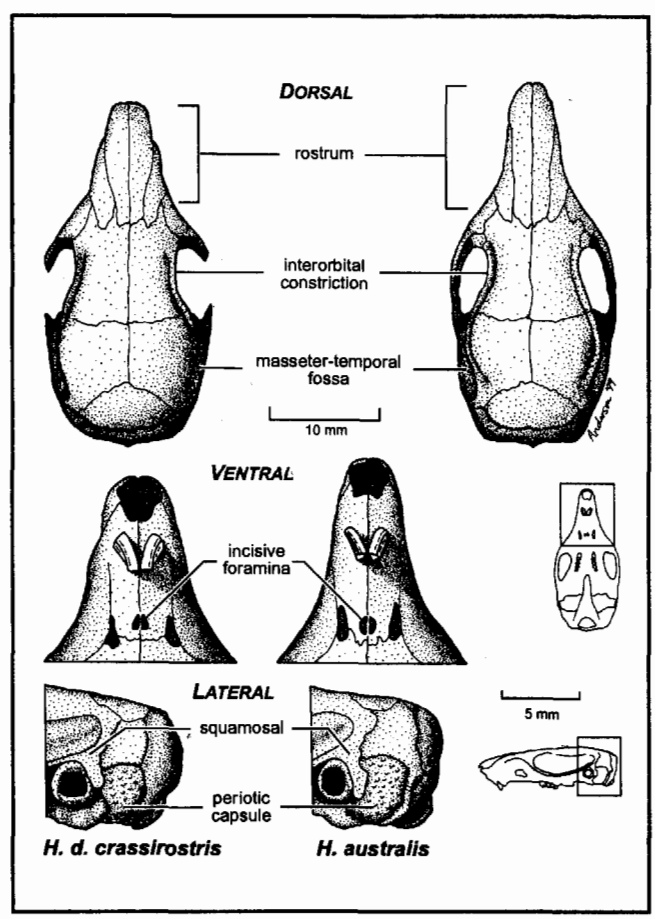

Figure 4. Crania of *Heteromys desmarestianus crassirostris* (*left*, IND-M 3645, Chocó: Alto de Barrigonal) and *H. australis* (*right*, IND-M 5034, Chocó: Alto del Limón) from northwestern Colombia: dorsal view (*upper*), ventral inset (*middle*), and lateral inset (*lower*). Both specimens are adult females in age class 4 **Rogers & Schmidly** (1982).

1, Fig. 2, Fig. 4). No single skull character is distinctive or unique for this species throughout its range, although its braincase is often noticeably inflated. Characters of the skull are best treated as comparisons between pairs of species.

Comparisons.—*Heteromys australis* is slightly larger than *H. d. crassirostris* and much smaller than *H. anomalus* (Table 1). Its slaty gray dorsal pelage distinguishes it from most other members of the genus, including *H. d. crassirostris* (which is chocolate brown) and *H. anomalus* (which in Colombia is light brown and strongly grizzled with ochraceous hairs). The tail of *H. australis* is shorter than that of *H. anomalus*. Whereas the tail of *H. australis* varies from moderately bicolored to nearly uniform, that of *H. anomalus* is almost always sharply bicolored. In addition, the ears of *H. australis* are smaller than those of *H. anomalus*.

Cranially, *Heteromys australis* differs from *H. anomalus* in several characters **Anderson & Soriano** (1999), Fig. 2). *H. australis* has a shorter and relatively broader skull than *H. anomalus* (Table 1). Its masseter-temporal fossae are not as well excavated as in *H. anomalus*. In general, its skull is not as robust as that of *H. anomalus*, and the braincase is usually inflated. In comparison with *H. d. crassirostris* (Fig. 4), *H. australis* has a slightly larger and more elongated skull, especially in the area of contact with *H. d. crassirostris*. In the Darién region, when compared to *H. d. crassirostris*, *H. australis* has more evenly bowed incisive foramina, much smaller palatal foramina, and a distinctively undulated posterior margin of the squamosal, which is caused by the large antero-dorsal lobe of the periotic capsule of the mastoid. The zygomatic arches are complete in adults but are often broken in museum specimens (Fig. 2). Similarly, the lacrimals frequently fall off cleaned skulls, and their presence is not useful as a taxonomic character.

Taxonomic review.—Three named taxa are synonyms of *Heteromys australis* Thomas: *Heteromys lomitensis* J. A. Allen, 1912 (from the Cordillera Occidental above Cali, Colombia), *Heteromys australis consicus* Goldman, 1913 (from eastern Panama), and *Heteromys australis pacificus* Pearson, 1939 (also from eastern Panama). **Allen** (1916), himself soon synonomized *H. lomitensis* with *H. australis*. Although some authors have since considered *H. lomitensis* a valid species, **Rodríguez-Mahecha *et al.*** (1995), my examination of museum specimens indicates that specimens from the type locality and other highland sites fully intergrade with specimens from the lowlands. I currently recognize no subspecies of *H. australis*.

A few *Heteromys australis*-like specimens from localities in Antioquia are not reported here. They agree with the external characters of *H. australis*, but display cranial proportions outside the variation that I currently accept for that species. Future museum work and morphometric analyses will examine their taxonomic status.

Known distribution.—*Heteromys australis* (Fig. 5) inhabits the wet lowland rainforests of the Chocoan (Pacific) coastal plain of western Colombia and extends up the slopes of the Andes to ca. 2000 m in sufficiently wet areas, but has not been collected in the drier intercordilleran valleys. The highest altitude I have confirmed for this species is 2450 m (Valle del Cauca: Municipio Dagua, El Jordán). *Heteromys australis* is known from both versants of the Cordillera Occidental, both faces of the Cordillera Central, and a few localities on the western slope of the Cordillera Oriental. In the west, it extends its distribution into the adjacent lowlands of Panama and Ecuador, and to the east a relict population recently was reported for the Cordillera de Mérida in Venezuela **Anderson & Soriano** (1999). I have reidentified the specimens reported from 1400 m on Cerro Pirre in eastern Panama **Rogers** (1990) as *H. d. crassirostris*.

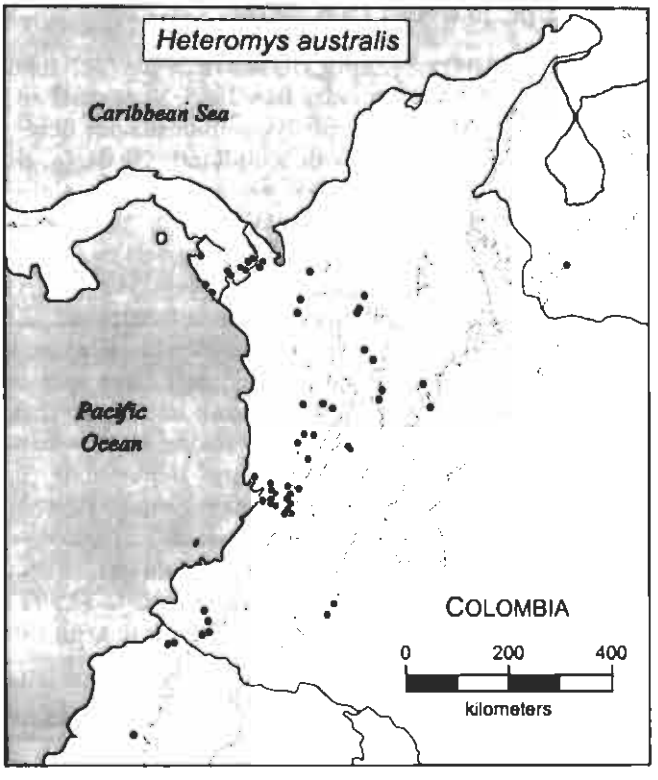

Figure 5. Map showing collection localities of *Heteromys australis* throughout its range (circles). Only georeferenced localities are shown here; see Appendix 1 for exact collection localities for all specimens examined.

but other nearby specimens do represent *H. australis* (Appendix 1). Contrary to **Eisenberg** (1989, 1999), the distribution of *Heteromys australis* extends only to eastern (not western) Panama. The westernmost locality I have confirmed for this species in Panama is near Puerto Indio (Darién: Esnápe).

Natural history.—Philip Hershkovitz (field notes) considered that at Antioquia: Valdivia, *Heteromys australis* appeared "to be semi-arboreal; at least they have been trapped on logs raised above but contacting the ground. The coastal form [*H. anomalus*] seemed to be strictly terrestrial." At the Tacarcuna localities in the Darién of eastern Panama, Charles Handley (field notes; specimen tags) took *H. australis* in forest, dry ridgetops, dry woods, dense bamboo, *Heliconia* thickets, and in dry grass and thorny bushes on an old river bar. They often were found on or under raised logs and near streams. **Allen & Barbour** (1923:264) noted that several individuals "lived in a series of holes in the stream bank near the Esnápe camp." They observed the mice during daylight hours on several occasions **Allen & Barbour** (1923). **Goldman** (1920) remarked that *H. australis* was mainly taken under logs in forest.

Heteromys desmarestianus crassirostris Goldman, 1912 Darién spiny pocket mouse

In this paper, I use the trinomial *Heteromys desmarestianus crassirostris* to refer provisionally to the populations of the *desmarestianus* complex present in northwestern Colombia. This small, dark species of the *desmarestianus* complex possesses chocolate brown dorsal fur that is slightly infused with paler ochraceous hairs, and the tail is rather short (averaging only slightly longer than head-and-body length, Table 1). Specimens from the cloud forests of the Darién have fairly soft dorsal pelage. The tail varies from moderately bicolored to mostly dark all around, and is usually mottled. The ears are small.

Cranially, this species is diminutive and gracile (Fig. 4). Its skull is very short and relatively broad (Table 1). The supraorbital ridges are weak, and the rostrum is distinctively short and wide (hence the name, *crassirostris*). The masseter-temporal fossae are barely indicated.

Comparisons.—*Heteromys desmarestianus crassirostris* is much smaller and darker than *H. anomalus* (Table 1). Its pelage is not markedly grizzled, and in Colombia, it is not as spiny as *H. anomalus*. In addition, the ears are much smaller than in *H. anomalus*. Its tail is also shorter than that of *H. anomalus*. Compared with *H. australis*, it is slightly smaller, and the dorsal pelage is somewhat glossy and chocolate brown instead of dull, slaty gray.

Cranially, the skull of *Heteromys d. crassirostris* (Fig. 4) is very small compared with that of *H. anomalus* (Fig. 2), which is larger, more elongated, and much more heavily ridged. *H. d. crassirostris* may be separated from *H. australis* in northwestern Colombia (Fig. 4) by its narrow, anteriorly converging incisive foramina, large palatal foramina (not illustrated), and straight posterior margin of the squamosal (with only a small antero-dorsal lobe of the periotic capsule of the mastoid). Although these characters consistently serve to distinguish these two species in the Darién, they do not necessarily characterize the species throughout their ranges.

Taxonomic review.—*Heteromys desmarestianus*, as currently used in the literature, includes multiple evolutionary species (**Anderson & Rogers,** unpublished data). The southeastern-most named form of the *desmarestianus* complex is *Heteromys crassirostris* Goldman, 1912 from Mount Pirri (= Cerro Pirre) in extreme eastern Panama. I herein use the trinomial *Heteromys desmarestianus crassirostris* to refer provisionally to the species of the *desmarestianus* complex that is present in northwestern Colombia. A future paper will revise the *desmarestianus* complex in southern Central America and confirm the valid name for this taxon. Although the presence of *H. desmarestianus* in South America was suspected as early as **Cabrera** (1960), **Cuervo-Díaz *et al.*** (1986:495) were the first to report it for Colombia. They gave "PNN Katíos," a national park in the lowlands next to Panama, as the locality for the specimens on which they based the report, but did not provide museum numbers. The only specimens from PNN Katíos that I am aware of are *H. australis* (Appendix 1). The presence of *H. desmarestianus crassirostris* in lowland habitats (below 1000 m), such as in the PNN Katíos, is unlikely.

Known distribution.—A species belonging to the *desmarestianus* species complex occurs in extreme northwestern Colombia, which I provisionally refer to as *Heteromys desmarestianus crassirostris* (see taxonomic review). This species is confirmed for Colombia from a single locality (Chocó: Serranía del Darién, Alto de Barrigonal) in the high reaches of the Serranía del Darién (Fig. 1) near the border with Panama, where it occurs on Cerro Tacarcuna, Cerro Mali, and Cerro Pirre. In Colombia, it is probably distributed above 1500 m in the Serranía del Darién as well as in the Alto de Nique (which is contiguous with the Pirre range in Panama). Its further distribution in Central America remains unclear.

Natural history.—Charles Handley's field notes indicate that, at Cerro Malí and Cerro Tacarcuna, this

species was collected primarily in cloud forest and along streams, often on or under logs and on rocks or under rock ledges. In moist situations on Cerro Mali (6000 ft.), it was the most abundant rodent. He considered this species partly diurnal. Similarly, **Goldman** (1920:117) reported the capture of *Heteromys d. crassirostris* at Mount Pirri (= Cerro Pirre) on the "densely forested upper slopes... under logs... and at holes in overhanging banks and in other sheltered places." Handley noted that the contents of the cheek pouches of these mice included: (1) *seeds*: small dry seeds (3–10 mm in diameter); small fleshy seeds; larger seeds, up to 25 mm; and winged seeds; (2) *nuts*: small nuts (pea sized); larger nuts, often fragmented; whole nuts, 8–12 mm in diameter; and a whole palm nut, 19 mm in diameter; (3) *fruits*: a soft, pea-sized fruit; and a plum-like fruit (10 mm in diameter); (4) *fungus*: pieces of fleshy/spongy fungus; (5) *insects and other arthropods*: fragments of the exoskeleton of a millipede; parts of a large centipede; 1 orthopteran leg; the leg of a large insect; a caterpillar; a live beetle; and another live beetle, 35 x 12 mm, with large anterior "pinchers," alive and pinching, head and thorax in one pouch, abdomen with wings in the other; (6) *small vertebrates*: vertebrae of small snake or lizard; small frog, entire but decomposed; another small frog; and the bones of a small bird (carrion); and (7) *other plant matter*: fragments of a fleshy root; a small, fleshy leaf; dry plant stems; a stem with small green buds; small flower heads with large ovary; and leaves and other litter. Presumably most of the contents of the cheek pouches were food material, but much of the vegetative contents were probably intended as nesting material. Stomach contents included a white mealy matter, insects, and nematodes.

Discussion

The distributions of *Heteromys anomalus* and *H. australis* are, in the broadest sense, quite simple. *Heteromys anomalus* is found across the northern (Caribbean) coast of Colombia and Venezuela in moderately dry areas of seasonal (deciduous) or semi-seasonal forests or agricultural areas, as well as occasionally in wet forest. On the other hand, *H. australis* inhabits the rainforested western (Pacific) coastal plain of northwestern South America as well as wet areas of the northern Andes up to ca. 2000 meters. Details of their distributions, however, present several biogeographic questions, most of which remain to be fully answered.

Distributional patterns

In addition to its coastal distribution, *Heteromys anomalus* is found in moderately dry areas of the upper valley of the Río Magdalena (Fig. 1, Fig. 3). Evidently, the specimens in the upper Magdalena belong to a disjunct relictual population, although the lack of specimens from the Magdalena Medio (between Mompós and Honda) may simply reflect a lack of collection effort. The Magdalena Medio is classified as "bosque húmedo tropical" and "bosque muy húmedo premontano" under the Holdridge Life Zone system **IGAC** (1988b), seemingly more appropriate habitat for *H. australis* than for *H. anomalus*. A relict population in the upper Río Magdalena would indicate that at some time during its history in South America, *H. anomalus* was distributed uninterruptedly from the Caribbean to the upper Magdalena before a wetter climate changed the habitat of the Magdalena Medio, making it unsuitable for *H. anomalus*. Future inventories in various habitats in the lowlands around Barracabermeja could help fill this important gap and contribute to the understanding of these biogeographic questions.

Conversely, the montane population of *Heteromys australis* in the Cordillera de Mérida (Figs. 1, 5) is hypothesized to be disjunct from those in western and central Colombia Anderson & Soriano (1999). A relictual population of *H. australis* (which is restricted to wet forests) in Mérida would provide evidence for range retraction in response to a drier climate at some time in its history, probably during the early Holocene **Anderson & Soriano** (*op. cit*). Thus, heteromyines almost certainly have been in South America long enough to experience both warming (wetter) and cooling (drier) climate changes.

Surprisingly, *Heteromys anomalus* has not been collected from the rain-shadowed valleys of the upper Río Cauca, Río Dagua, or Río Patía in western Colombia. Environmental conditions in these valleys seem to match those for other localities where *H. anomalus* has been collected in Colombia. Because the geographic region of the valley of the Río Cauca has seen extensive collecting, I interpret the lack of specimens from this area as an indication that *Heteromys anomalus* probably never dispersed there. This suggests that the dry forests of the upper Magdalena had a more recent connection with those of the Caribbean coast than have those of the Río Cauca. The upper reaches of the Río Dagua and Río Patía are more distantly separated from Caribbean dry forest than the Río Cauca valley is; thus, *H. anomalus* probably never colonized those valleys either. The distribution of *H. anomalus* in Colombia is similar to that of the cotton rat, *Sigmodon hispidus*, which is present in the upper Magdalena, but not in the upper reaches of the Río Cauca, Río Dagua, or Río Patía **Voss** (1992). In

contrast, another sigmodontine rodent characteristic of non-forest habitats, *Zygodontomys brunneus*, is distributed in all four of these dry enclaves **Voss** (1991).

Unlike those two grassland species, no specimens of *Heteromys* are known from the open *llanos* (tropical grasslands) east and south of the Andes, in either Colombia or Venezuela. This absence is in spite of the fact that *H. anomalus* inhabits the gallery forests that infiltrate the *llanos* in Venezuela **Anderson & Soriano** (1999)—see lowland localities in Barinas). Evidently, although *H. anomalus* is tolerant of dry forest and agricultural habitats, it is not well suited to open grasslands.

Similarly, no *Heteromys* has been collected from Amazonian forests east of the Andes, even though *H. australis* inhabits very similar forests in the lowland Chocó of western Colombia. Furthermore, *H. australis* is present in wet forests (field notes, Philip Hershkovitz) at a low pass at the extreme southern end of the Cordillera Oriental (Huila: Río Suaza, Río Aguas Claras, near San Adolfo). These forests historically were fully connected with the wet forests of Putumayo and Caquetá in the Amazon basin just to the east (**Miller,** 1918:96–97). The evident failure of *H. australis* to descend through the piedmont into the expanse of Amazonia remains puzzling. Perhaps some elements of the more diverse Amazonian fauna competitively exclude *H. australis* and prevent its successful colonization of that region.

Future inventories will increase our understanding of these and other small mammals. The confirmed localities for these species point to several areas where *Heteromys* should be present but have not been collected. As mentioned before, either *H. australis* or possibly *H. anomalus* is probably present in the humid lowlands of the Magdalena Medio; specimens from this region would help resolve the question of whether the *H. anomalus* of the upper Río Magdalena represent a disjunct population. Similarly, many gaps exist in the known distribution of *H. australis* in Colombia. Surprisingly, no specimens are known to me from the Departamento del Cauca (between Nariño and Valle del Cauca in southwestern Colombia); *H. australis* should be present there in both humid lowlands and montane regions. The destruction of most of the mammal collection of the Universidad del Cauca in the Popayán earthquake of 1983 created a geographic gap in collection coverage for the country that is in need of filling.

The distribution of *Heteromys australis* is especially under-sampled in the eastern part of its range, however. Outside the western half of its distribution—the Chocoan lowlands, the Cordillera Occidental, and the Cordillera Central— this species is known from only three localities in the Cordillera Oriental of Colombia (Huila: San Adolfo and vicinities; Cundinamarca: Paime; and Boyacá: Serranía de la Quinchas) and one locality in the Cordillera de Mérida in Venezuela. I predict that it will eventually be found in appropriate habitats at intermediate elevations along most of the western slopes of the Cordillera Oriental. Furthermore, its presence in the Pregonero region of the Cordillera de Mérida **Anderson & Soriano** (1999) suggests that *H. australis* may inhabit part of the eastern versant of the Cordillera Oriental as well. These intermediate altitudes of the northern half of the Cordillera Oriental represent one of the many biologically undersampled regions of Colombia. In the future, systematists and biogeographers will find much fruitful field and museum research to conduct on the small mammals of this and other areas of the northern Andes. *Heteromys d. crassirostris*, the only species of the *desmarestianus* complex present in South America, shows a distribution restricted to areas west of the Río Atrato-Río San Juan lowlands, similar to that of pocket gophers (Geomyidae), another rodent group that originated in North America **Alberico** (1990). Thus, the distribution of the *desmarestianus* group lends further evidence to the role of the Bolivar Trough and the present-day Río Atrato-Río San Juan lowlands as a filter to fuanal exchange between North and South America **Alberico** (1990).

Phylogenetic affinities and colonization of South America by heteromyines

Rogers (1990) presented data on allozymic variation from the analysis of proteins at 30 presumptive gene loci for species of the subfamily Heteromyinae (genera *Heteromys* and *Liomys*). For the southern species of the subfamily, his study included two samples from eastern Panama and two from Venezuela. The taxonomic review herein allowed me to confirm the identities of the tissue vouchers from Panama (the LSUMZ specimens that correspond to the genetic tissue samples Rogers analyzed). Locality 27 from **Rogers** (1990) represents *Heteromys australis*, and Locality 26 is the species that I here refer to as *H. d. crassirostris* (see Results and Appendix 1). Phenetic analyses **Rogers** (1990) indicated that the specimens from Locality 26 (*H. d. crassirostris*) are similar to specimens from Costa Rica (Localities 16 and 17) referred to as *Heteromys* sp. in **Rogers** (*op. cit*). In the future, **Anderson & Rogers** (unpublished data) will review the taxonomy and biogeography of these species of the *desmarestianus* complex.

Likewise, based on allozyme data, specimens from Locality 27 (*Heteromys australis*) are most similar to

specimens of *H. anomalus* from Localities 24 and 25 in Venezuela **Rogers** (1990). Therefore, the two species of *Heteromys* with broad distributions in South America (*H. anomalus* and *H. australis*) may be sister species, and certainly are closely related. Thus, except for *H. d. crassirostris*—which has only a marginal distribution in South America to the west of the former Bolivar Trough—the species of *Heteromys* inhabiting the main continental area of South American species may be monophyletic, raising the possibility that heteromyines colonized South America only once. Future studies reviewing the spiny pocket mice of the rest of South America will determine whether any other species are present in addition to those discussed here. Further speculation on the colonization of this southern continent by *Heteromys* is premature until such studies are completed. In the future, techniques of molecular genetics, such as DNA sequencing, should be applied along with cladistic methods of data analysis in order to elucidate the phylogenetic relationships of these rodents and reveal more details of their evolution and biogeography.

Conservation status

Although none of these spiny pocket mice likely suffers from significant threats to its immediate survival, human impact in the past half-century has undoubtedly affected each in ways that we will never fully understand. *Heteromys anomalus* (Philip Hershkovitz's field notes from 1942) tolerates and, indeed, thrives in association with traditional low-density human agricultural settings (see account of that species). Native small rodents are affected negatively by the application of chemicals in agricultural areas **Bonaventura *et al.*** (1988), however. Such effects have not been explicitly studied in Colombia, and *H. anomalus* may no longer inhabit agricultural areas at the high densities it did before the widespread use of agrochemicals. Recently, *H. anomalus* was captured only sporadically in degraded vegetation within an agricultural matrix in northern Colombia, **Adler *et al.*** (1997), in contrast to Hershkovitz's findings. However, these studies are not directly comparable, employing different methodologies, trapping effort, expertise, and duration; this situation emphasizes the difficulties in comparing surveys undertaken by different collectors in different eras and the value of standardized inventory methods.

The historical distribution of *Heteromys australis* probably has been reduced more by humans than that of *H. anomalus*. While *H. anomalus* can survive well in rural settings, it appears that *H. australis* is restricted to relatively undisturbed forest environments. Even though large expanses of suitable habitat still exist—especially in the Chocó—populations of *H. australis* in the Andes undoubtedly have experienced extreme fragmentation of their habitat in the last 50 years. Although the long-term effects of fragmentation are unknown, theoretical models of metapopulation dynamics and island biogeography clearly predict reduced chances of long-term survival for species with less, smaller, and farther-separated populations, **Meffe & Carroll** (1997).

Finally, *Heteromys d. crassirostris*, which inhabits the extremely rugged and remote Darién, is likely largely insulated from the effects of humans. This region, however, has long been slated for completion of the Pan-American highway linking North and South America. Although this road through the lowlands is unlikely to be built in the immediate future, the increased access and human population density produced by the highway would eventually lead to more intensive settlement of and extraction of natural resources from the higher elevations of the Darién, where *H. d. crassirostris* is found.

The role of museum collections in studies of biodiversity

The research collections of natural history museums and herbaria constitute an immense source of raw data for studies of comparative biology and patterns of biodiversity. This study illustrates the critical nature of careful and competent systematic revision of species limits and specimen identification before embarking on such projects. The *Heteromys* of South America, like many genera of rodents, have not been critically revised in the last 60–90 years (*i.e.*, since **Goldman** (1911, in this case). Since that time, holdings of scientific collections have doubled many times, but systematic understanding of the southern species of the group has not increased accordingly. Even professional systematic mammalogists commonly misidentify specimens outside their genera of specialty, moreso if no recent comprehensive revision exists. Few groups of Neotropical small mammals have been sufficiently revised to allow identification by non-systematists. Approximately one-third of the specimens I examined from Colombian localities did not bear correct identifications. Museums in Colombia and the United States possessed similar rates of misclassification. Many were problems of synonymy (accepting *H. jesupi* and *H. lomitensis* as valid species, for example). Additionally, large numbers of specimens were identified only to genus, which perhaps was often the most responsible identification to give them.

Myriad other errors were present as well. Especially common were specimens of *Heteromys australis* iden-

tified as *H. anomalus,* sometimes hundreds of kilometers from areas where *H. anomalus* is actually found. Some large series of *H. australis* from the Andes were cataloged as *H. desmarestianus*. Even correcting for problems of synonymy, the original identifications clearly would have painted a quite different—and false—picture of the distributional patterns presented here. Initiatives to proof data bases, model species distributions using predictive analyses, and conduct meta-analyses of patterns of biodiversity currently are currently being undertaken for the birds **Peterson, *et al.*** (1998 a, b). mammals, and butterflies of Mexico. These approaches hold enormous promise and should be emulated in other countries with a wide variety of appropriate taxa and carefully verified identifications of museum specimens.

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Appendix 1: Gazetteer of localities for specimens examined

The specimens from the following localities constitute the basis of this report. For *Heteromys anomalus*, I list all verified specimens that I have examined from Colombia. For *H. australis*, I present all specimens from the entire distribution known to me for that species. For the species I here provisionally refer to as *H. desmarestianus crassirostris*, I include only those specimens from the Darién region that I can confidently establish as conspecific with the name *Heteromys crassirostris* Goldman. *Departamentos*, *Estados*, and *Provincias* appear in *italics*. Additionally, the first phrase of each locality is given in **bold.** Latitude (degrees and minutes) north of the equator and longitude (degrees and minutes) west of Greenwich are given without punctuation (*e.g.*, 0735/7512 for 7°35'N, 75°12'W). Localities south of the equator are denoted with an S after the four digits for latitude. All secondary information provided by sources other than the collector are included in [brackets] followed by the source. Museum catalogue numbers for specimens examined are given at the end of each locality using the abbreviations provided in the methods section.

***Heteromys anomalus*.—COLOMBIA (total 214): *Antioquia,* Caucasia,** 12 km S (Hacienda Barro), 250 m [0753/7512, IGAC, 1989a (not Voss, 1991)], USNM 449537–449538. **Urabá,** Río Currulao, 50 m [0800/7644, Hershkovitz, 1977], FMNH 70473. ***Atlántico,* Ciénaga de Guájaro,** Sabana Larga [15 m, 1037/7502, Hershkovitz, 1947], USNM 280209–280213. ***Bolívar,* Río San Pedro,** Norosí, Mompós [180 m, 0838/7404, Hershkovitz, 1977], USNM 280298. **San Juan Nepumuceno,** 167 m [0958/7504, Hershkovitz, 1977], FMNH 69225–69235. ***Cesar,* Colonia Agrícola de Caracolicito,** Santa Marta, 400 m [1018/7400, Hershkovitz, 1947], USNM 280214–280250. **El Salado** [430 m, 1022/7329, Hershkovitz, 1947], USNM 280254–280269. **Pueblo Bello** [1067 m, 1024/7339, Hershkovitz, 1947], USNM 280251–280253. **Pueblo Viejo,** 8000 ft. [1059/7327 in the Departamento de La Guajira (IGAC, 1988; Paynter, 1997) Musser *et al.*, 1998 (not Paynter, 1997)], MCZ B8072, B8074; USNM 85543. **Valledupar,** El Guaimaral [140 m, Hershkovitz, 1947], [1014/7330, Voss, 1991], USNM 280270–280277. ***Córdoba,* Catival,** upper Río San Jorge, 120 m [0817/7541, Hershkovitz, 1977], FMNH 69243–69256. **Montería,** Granja Turipaná, 15 m [coordinates for Montería are ca. 0846/7553, Paynter, 1997], UV 8435, 9830–9031. **San Andrés de Sotavento** [0908/7532, Adler *et al.*, 1997], UV 11239. **Socorré,** upper Río Sinú, 100 m [0751/7617, Hershkovitz, 1977], FMNH 69236–69239. ***Cundinamarca,* Caparrapí,** Volcanes [250 m, Hernández-Camacho, 1956], [0527/7431, IGAC, 1973 (not Hernández-Camacho, 1956; Musser *et al.*, 1998; Voss, 1992)], ICN 409, 1827–1831, 1832—holotype of *Heteromys anomalus hershkovitzi* [= No. 2701 of former Instituto Carlos Findlay], 1833–1835,1866; MLS 2173. **Ricaurte,** Vereda El Callejón, 350 m [ca. 0418/7443, IGAC, 1989c], ICN 12575–12576, 12882–12884. ***La Guajira,* Las Marimondas,** E. Andes, Fonseca [1000 m, 1052/7243, Hershkovitz, 1947], USNM 280293–280297. **Mamorongo,** 3000 ft. [ca. 1057/7318, Paynter, 1997], MCZ B8358. **San Francisco,** 6000 ft. [but see Paynter, 1997], [1100/7326, Paynter, 1997], MCZ B8359. **San Miguel** [1700 m, 1058/7329, Paynter, 1997], MCZ B8265. **Serranía La Macuira** [exact coordinates not available], IND-M 5924. **Sierra Negra,** Villanueva, Valledupar, 1500 m [1036/7255, Hershkovitz, 1960], USNM 280278–280282. **Villanueva,** Valledupar, 280 m [1037/7258, Hershkovitz, 1947], USNM 280283–280292. ***Magdalena,* below Minca,** 1000 ft. [ca. 1109/7407, Paynter, 1997], AMNH 15347—holotype of *Heteromys jesupi*, 15348. **Bonda** [ca. 150 ft., 1114/7408, Paynter, 1997], AMNH 15352–15354. **Buritaca** [sea level, 1115/7346, Paynter, 1997], AMNH 23318; FMNH 13233. **Don Diego,** 5 m [1115/7342, Paynter, 1997], FMNH 13234–13235, 44864. **El Líbano Plantation,** 500 ft. [exact coordinates not available], AMNH 15349–15350. **Mamatoca,** 100 ft. [1114/7410, Paynter, 1997], AMNH 15351. **Masinga Vieja,** 500 ft. [ca. 1116/7405, Paynter, 1997], AMNH 15356. **Minca,** 2000 ft. [1109/7407, Paynter, 1997], AMNH 15344–15346, 15493, 23320. **Olimpia,** 2500 ft. [coordinates not available], AMNH 23319. **Onaca** [680 m, 1111/7404, Paynter, 1997], AMNH 15355, 23632. **Palomino** [ca. 600 m, 1102/7339, Paynter, 1997], MCZ B8255–B8258, B8260–B8264, B8351–B8357; USNM 85542. **Santa Marta,** Alto de Mira, 3 km W del Río Buritaca, Sierra Nevada de Santa Marta, 1050 m [ca. 1108/7354, IGAC, 1975], ICN 13010. **Santa Marta,** Parque Nacional Natural Tayrona, El Cedro, 420 m [1119/7401, Garcés-Guerrero & De la Zerda-Lerner, 1994; IGAC, 1975], ICN 9053–9055; IND-M 2783, 4178, 4885. ***Norte de Santander,* Corregimiento de La Donjuana** (Hacienda La Selva) [ca. 1100 m, ca. 0745/7235, Paynter, 1997], MLS 2048–2049. **Durania,** Finca La Palma [coordinates for Durania are ca. 0743/7240, IGAC, 1985c], ICN 10974. **Guamalito,** El Carmen [ca. 600 m, ca. 0834/7327, Hershkovitz, 1947], USNM 280299–280304. **Río Tarrá,** San Calixto [ca. 200 m, 0836/7301, Hershkovitz, 1947], USNM 280305–280306. ***Sucre,* Colosó,** Las Campanas, 175–350 m [0930/7521, Hershkovitz, 1977], FMNH 69240–69242. ***Tolima,* Chicoral,** Coello River, 1800 ft. [0413/7459, Paynter, 1997], AMNH 32965. **Honda,** Magdalena River, 600 ft. [0512/7445, Paynter, 1997], AMNH 34593. **Melgar** [430 m, ca. 0412/7439, Paynter, 1997], ICN 4402–4403. Plus hundreds of specimens from Venezuela and Trinidad & Tobago.

***Heteromys australis*.—COLOMBIA (total 177): *Antioquia,* Alto Bonito,** 1500 ft. [elevation erroneous in Paynter, 1997], [0705/7630, Paynter, 1997], AMNH 37744. **Bellavista,** 4 km NE, above Río Porce, 1200 m [ca. 0626/7520, Hershkovitz, 1977], FMNH 70471–70472. **Guatapé,** 1880 m [ca. 0614/7510, IGAC, 1989a], UV 7052–7056. **La Frijolera,** 5000 ft. [ca. 0710/7525, Paynter, 1997], AMNH 37745. **Purí,** above Cáceres, 200 m [0725/7520, Hershkovitz, 1960], FMNH 70470. **Urabá,** Villa Arteaga, 130 m [0720/7626, Hershkovitz, 1977], FMNH 70483–70485. **Valdivia,** 9 km S, 1200–1700 m [0706/7528, IGAC, 1989a], FMNH 70459–70464, 70474–70479. **Valdivia,** 10 km S, 1500–1700 m [0706/7528, IGAC, 1989a], FMNH 70465–70467, 70480–70481. **Valdivia,** La Selva, 1900 m [0706/7528, IGAC, 1989a], FMNH 70469. **Valdivia,** Quebrada Valdivia, 900 m [0710/7526, IGAC, 1989a], FMNH 70468. **Valdivia,** Ventanas, 2000 m [0705/7527, IGAC, 1989a], FMNH 70482. ***Boyacá,* Municipio Puerto Boyacá,** Corregimiento Puerto Romero, Vereda Puerto Zipa, Serranía Las Quinchas, 1175 m [0549/7418, IGAC, 1989b], ICN 13150–13151. ***Caldas,* Municipio Samaná,** Corregimiento Florencia, bosques de Florencia, sito El Estadero, 1850 m [ca. 0531/7504, ICAC, 1985a], IND-M 5751–5756. **Samaná,** Río Hondo, 1100–1400 m [0542/7501, Hershkovitz, 1997], FMNH 71185–71190. ***Chocó,* Bagadó,** 1000 ft. [but see Paynter, 1997], [ca. 0525/7624, Paynter, 1997], AMNH 34138. **Municipio Riosucio,** Vereda Peye, Alto Limón, sobre muro fronterizo, Parque Nacional Natural Los Katíos [0756/7710, Garcés-Guerrero & De la Zerda-Lerner, 1994; IGAC, 1985b], IND-M 5032–5038. **Parque Katíos,** Alto del Limón, 600 m [0756/7710, Garcés-Guerrero & De la Zerda-Lerner, 1994; IGAC, 1985b], IND-M 3883. **San José del Palmar,** Alto de Oso, Corregimiento La Italia, 1000 m [0454/7623, IGAC, 1985b], UV 10129, 10866. **Unguía,** upper Río Ipetí, ca. 0 m [0801/7707, Hershkovitz, 1977], FMNH 70486–70487. ***Córdoba,* Socorré,** upper Río Sinú, 100–150 m [0751/7617, Hershkovitz, 1977], FMNH 69257–69262. ***Cundinamarca,* Paime** [1038 m, ca. 0522/7410, Paynter, 1997], AMNH 70582, 71256; MLS skin #2303. ***Huila,* Acevedo,** San Adolfo, 1400 m [0149/7552, Paynter,

1997], FMNH 71208–71210. **Río Suaza,** Río Aguas Claras, near San Adolfo, 1400–1600 m [0137/7559, Paynter, 1997], FMNH 71191–71207. ***Nariño,*** **Barbacoas** [35 m, 0141/7809, Paynter, 1997], AMNH 34178–34180, 34182, 34184–34185. **Buenavista,** 1200 ft. [0129/7805, Paynter, 1997], AMNH 34181, 34183, 34186–34188. **Junín,** Planada de Maindés, 870 m [0115/7810, Orejuela-Gartner *et al.*, 1982], UV 3067–3069, 3040A. **Municipio Barbacoas,** Corregimiento Altaquer, ca. 7 km NE Altaquer, Reserva Natural del Río Ñambí (FELCA), 1300 m [0118/7803, Cadena *et al.*, 1998], ICN 13659. ***Quindío,*** **El Roble,** Quindío Andes, 7200 ft. [0441/7536, Paynter, 1997], AMNH 32960–32962, 32964; MCZ 17312. **Filandia,** Finca Bremen-La Popa, 1950 m [ca. 0440/7537, IGAC, 1978, 1982a], ICN 11656. **Salento,** W. Quindío Andes, 7000–7100 ft. [0438/7534, Paynter, 1997], AMNH 32958–32959, 32966. ***Risaralda,*** **Mistrató,** Corregimiento de Puerto de Oro, Finca la Esparta, sitio Rincón Puto, cerca a la Laguna del Oso, 1300 m [ca. 0527/7604, IGAC, 1988a (not IGAC, 1982b)], ICN 11944. **Mistrató,** Vereda Empalado, Km 12 carreterra Mistrató-San Antonio de Chamí, 1900 m [ca. 0522/7553, IGAC, 1988a (not IGAC 1982b)], ICN 12712. **Mistrató,** Vereda La Jalea, Km 8 carreterra Mistrató-San Antonio de Chamí, 1720 m [ca. 0521/7553, IGAC, 1988a (not IGAC, 1982b)], ICN 12713. **Pereira,** La Suiza, 1950 m [0444/7535, IGAC, 1988a (not IGAC 1982b)], ICN 12103. ***Valle del Cauca,*** **Alto Anchicayá,** 600 m [ca. 0336/7654, IGAC, 1982c], USNM 554229. **Bahía Málaga,** Quebrada Valencia, camino a Quebrada Alegría, 0–60 m [0407/7714, IGAC, 1982c], UV 5406, 5408–5409, 5519–5521. **Bolívar,** 10 km N, 15 km W (Municipio Bolívar, Finca El Manzano, Betanica), 0426/7619 [from specimen tag], UV 3949. **Bosque San Antonio** (Km 18 carretera Cali-Buenaventura) [2000 m, 0330/7638, Alberico, 1983], UV 2215. **Buenaventura,** 14 km E (Río Dagua) [0352/7657, IGAC, 1982c], USNM 483975. **Buenaventura,** Bajo Anchicayá, 230 m, 0337/7656 [from specimen tag], UV 10507. **Buenaventura,** Corregimiento de Llano Bajo, carretera vieja a Buenaventura, ca. 50 m [0342/7658, Alberico, 1983], UV 2216. **Buenaventura,** Planta acueducto Río Escalerete, ca. 50 m [0350/7654, Alberico, 1983], UV 3215–3216. **Buenaventura,** Río Raposo, ca. 0 m [0341/7705, Alberico, 1983], UV 4906–4909, skin #4910, 4911–4913. **Dagua,** Morro Frío [0344/7640, M.S. Alberico, *in litt.*, May 1999], UV 11170. **Darién** (= Calima), Estación Río Azul, márgen derecho Río Calima, 500 m [0357/7640, IGAC, 1982c], ICN 8729–8730. **El Silencio** [1500 m, 0348/7637, Alberico, 1983], UV 6033. **El Tigre,** Río Raposo, ca. 0 m [ca. 0341/7705, Alberico, 1983], ICN 4377, 4380. **Granja Agroforestal Bajo Calima,** 40 m [0400/7656, González-M. & Alberico, 1993 (not Paynter, 1997)], UV 2832–2833, 4083–4084. **Las Lomitas,** 5000 ft. [0338/7638, Paynter, 1997], AMNH 32240—holotype of *Heteromys lomitensis*. **Municipio Buenaventura,** Concesión Bajo Calima, Cuartel B-V-83 [40 m, 0400/7656, Alberico, 1983 González-M & Alberico, 1993 (not Paynter, 1997)], UV 5926–5930, 7396, 10963. **Municipio Dagua,** El Jordán, 2450 m [0332/7640, Alberico, 1983], UV 9713. **Peñas Blancas,** Río Pichindé, ca. 1800 m [ca. 0327/7643, Paynter, 1997], USNM 507222. **Pichindé,** ca. 1900 m [coordinates for Pichindé are ca. 0327/7637, IGAC, 1982c (not Alberico, 1983)], UV 6028, 6030–6031, 6035–6038, 6644. **Pichindé,** Finca Bellavista [1800 m, Alberico, 1983], [coordinates for Pichindé are ca. 0327/7637, IGAC, 1982c (not Alberico, 1983)], UV 6034. **Pichindé,** Finca La Flora, 1800–1900 m [coordinates for Pichindé are ca. 0327/7637, IGAC, 1982c (not Alberico, 1983)], ICN 4378–4379, UV 6032. **Reserva Forestal Yotoco** [1500 m, 0353/7628, Alberico, 1983], ICN 6896; UV 2047. **Río Raposo Virology Field Station** [0338/7705, Musser *et al.*, 1998], USNM 334697. **Zabaletas,** ca. 5 km W (old road to Buenaventura), ca. 50 m [0347/7659, IGAC, 1982c], USNM 507223. ***Valle del Cauca-Chocó,*** **Alto de Galápagos,** 2000 m, 0453/7613 [from specimen tag], UV 4459. **ECUADOR (total 11):** ***Esmeraldas,*** **Bulím** [= Pulún], N. Ecuador, 50 m [0105/7840, Paynter, 1993], FMNH 18871, USNM 172940. **San Javier,** N. Ecuador, 60–120 ft. [topotypes of *Heteromys australis*], [ca. 0104/7847, Paynter, 1993], USNM 113304–113307. ***Los Ríos,*** **Río Palenque Biological Station,** 220 m [0034S/7920, Lynch & Duellman, 1997], KU 149132–149135. **Río Palenque Science Center,** 47 km S (by road) Santo Domingo [0034S/7920, Lynch & Duellman, 1997], USNM 528573. **PANAMA (total 110):** ***Darién,*** **Amagal,** 1000–2000 ft. [0724/7802, Fairchild & Handley, 1966], ANSP 19491–19498, 19499—holotype of *Heteromys australis pacificus*, 19779. **Boca de Río Paya** [0755/7731, Fairchild & Handley, 1966], USNM 314580. **Ca. 6 km NW Cana,** E. slope Cerro Pirre, 1200 m [ca. 0751/7744, Fairchild & Handley, 1966], LSUMZ 25452. **Cana,** 1800–2000 ft. [0747/7742, Fairchild & Handley, 1966], USNM 178621, 178698, 178699—holotype of *Heteromys australis consicus*, 178700, 179595. **Esnápe** [0805/7813, Fairchild & Handley, 1966], MCZ 19828. **Junction Río Jaqué-Río Imamado** lies at ca. 0734/7754 (SCDEC, 1957), USNM 363181–363182. **La Laguna** [3200 ft., 0804/7719, Fairchild & Handley, 1966], KU 99367. **Near Río Setegantí,** 1500–3400 ft. [0746/7740, Fairchild & Handley, 1966], USNM 318152–318171. **Paya Camp** [0753/7724, Fairchild & Handley, 1966], USNM 314579. **Río Paya** (mouth) [0755/7731, Fairchild & Handley, 1966], USNM 306899–306900. **Tacarcuna** [exact coordinates not available], KU 99368–99375. **Tacarcuna Casita Camp,** 2700–2800 ft. [0801/7722, Fairchild & Handley, 1966], USNM 310389–310396, 310446. **Tacarcuna Laguna Camp,** 4000 ft. [0804/7719, Fairchild & Handley, 1966], USNM 310433. **Tacarcuna Village** [0805/7717, Fairchild & Handley, 1966], UMMZ 165328–165329. **Tacarcuna Village Camp,** 3200 ft. [0805/7717, Fairchild & Handley, 1966], USNM 310397–310432, 310434–310445. **VENEZUELA (total 1):** ***Táchira,*** **Presa La Honda,** 10 km SSE Pregonero, 1100 m [ca. 0757/7142, MARNR, 1996], CVULA-I 3503.

Heteromys desmarestianus crassirostris.—**COLOMBIA (total 6):** ***Chocó,*** **Límite Colombo-panameño, Serranía del Darién, Alto de Barrigonal** is a cerro in the upper reaches of the Río Unguía near the border with Panama (J.V. Rodríguez, *in litt*, August 1999); from IGAC (1985b), this site is located near 0803/7715, IND-M 3643–3648. **PANAMA (total 253):** ***Darién,*** **4 miles W of Cerro Mali** on ridge, 4800 ft. [exact coordinates not available], UMMZ 165330. **Ca. 6 km NW Cana,** Cerro Pirre (E. slope), 1400 m [ca. 0751/7744, Fairchild & Handley, 1966], LSUMZ 25450–25451. **Ca. 7 km NW Cana,** Cerro Pirre (E. slope), 1500 m [ca. 0751/7744, Fairchild & Handley, 1966], LSUMZ 25449, 25453–25454. **Cerro Mali** [0807/7714, Fairchild & Handley, 1966], UMMZ 165331–165332. **Cerro Mali,** 4700 ft. [0807/7714, Fairchild & Handley, 1966], USNM 338180–338191. **Cerro Tacarcuna,** 4100–4800 ft. [0810/7718, Fairchild & Handley, 1966], USNM 338192–338198. **Loma Cana,** 4900–5600 ft. [exact coordinates not available], ANSP 19507–19513, 19582–19594. **Mount Pirri,** 4700–5400 ft. [0751/7744, Fairchild & Handley, 1966], ANSP 19514–19527, 19529–19561, 19595–19662, 19775, 19777–19778, 19838–19840. **Mount Pirri,** 20 mi. S of, 5000 ft. [exact coordinates not available], ANSP 19563–19581, 19663–19666. **Mount Pirri,** near head of Río Limón, 4500–5200 ft. [0751/7744, Fairchild & Handley, 1966], FMNH 53994–53995; USNM 178998–179004, 179006–179015, 179016—holotype of *Heteromys crassirostris*, 179018–179020. **Mount Pirre Range,** "Rancho Plastico" above INRENARE station, Darién National Park, 1150 m [exact coordinates not available], USNM 565915–565916. **Mount Tacarcuna** [= Cerro Mali, see Fairchild & Handley, 1966], 5200 ft., [0807/7714, Fairchild & Handley, 1966], AMNH 37923. **Tacarcuna Mali Camp,** 5900 ft. [ca. 0807/7714, Fairchild & Handley, 1966], USNM 310447–310486.

Appendix 2: List of measured specimens

The following specimens form the samples for which mensural data are reported in Table 1. Museum abbreviations are as provided in methods section.

Heteromys anomalus

COLOMBIA (total 26): *Cesar,* Colonia Agrícola de Caracolicito, Santa Marta, 400 m: USNM 280214–280215, 280218–280221, 280223–280224, 280228–280229, 280231–280235, 280237–280244, 280247–280249.

Heteromys australis

COLOMBIA (total 12): Antioquia, Valdivia, 9 km S, 1200–1400 m: FMNH 70459–70461, 70463–70464, 70476–70478. Valdivia, 10 km S, 1500 m: FMNH 70467, 70480–70481. Valdivia, Quebrada Valdivia, 900 m: FMNH 70468.

Heteromys desmarestianus crassirostris

PANAMA (total 34): Tacarcuna Mali Camp, 5900 ft.: USNM 310448–310461, 310464–310470, 310472–310477, 310479–310483, 310485–310486.Table 1. External and cranial measurements (mm) for adult *Heteromys* of age classes 4 and 5 (Rogers & Schmidly, 1986) from selected localities in Colombia and Panama. See Appendix 2 for exact localities and specimen numbers. Statistics are given as mean ± one standard error, sample size, and (minimum–maximum).