

Map 21 Selected localities for *Orthogeomys dariensis* (●). Range in Panama from hall (1981). Contour line = 2,000 m.

height of the external auditory meatus in all three specimens of *O. dariensis* exceeded 2.3 mm, which also was considered diagnostic of *O. thaeleri* by Alberico (1990). The fact that *O. thaeleri* and *O. dariensis* have been collected within 100 km of each other in what appears to be continuous habitat suitable for pocket gophers leads me to conclude that *O. thaeleri* is simply a southward extension of *O. dariensis*.

Family Heteromyidae Gray, 1868

Robert P. Anderson

Three subfamilies comprise the Heteromyidae, but only one of them occurs in South America. Whereas the Dipodomysinae (kangaroo rats and kangaroo mice) and Perognathinae (pocket mice, both silky and coarse-haired) occur exclusively in North America, the Heteromyinae (spiny pocket mice) range from southern Texas, United States, to central Ecuador (Patton 2005a). Heteromyines represent a well-defined monophyletic group distinct from the two other subfamilies (M. S. Hafner 1981; J. C. Hafner and Hafner 1983; Wahlert 1991; J. C. Hafner et al. 2007). Of the two currently recognized genera of

heteromyines, only the genus *Heteromys* inhabits South America.

Modern usage of the genera *Heteromys* and *Liomys* began a century ago. After a rather turbulent taxonomic history of the subfamily during the nineteenth century (see account of the genus *Heteromys*), Merriam (1902) espoused recognition of two genera: *Heteromys* Desmarest, and *Liomys*, which he described. Soon thereafter, Goldman (1911b) accomplished the first comprehensive revision of the subfamily, providing emended diagnoses of the two genera and using these to place previously described species into their appropriate genera. Subsequent twentieth-century authors reviewing the taxonomy of heteromyines (e.g., Genoways 1973; Hall and Kelson 1959; Hall 1981; D. F. Williams et al. 1993; Patton 1993, 2005a) continued to recognize the two genera, which can be identified based on several diagnostic characters and which inhabit markedly different habitats, with species of *Heteromys* generally found in wetter, denser forests (R. P. Anderson et al. 2006).

However, substantial morphological diversity exists in *Liomys* (Genoways 1973), and recent phylogenetic studies have recovered three clades in the subfamily (*Heteromys*; the *adpersus-salvini* clade of *Liomys*; and the *irroratus-pictus-spectabilis* clade of *Liomys*), based on mtDNA sequences (Rogers and Vance 2005; J. C. Hafner et al. 2007) and allozymes and morphology (R. P. Anderson et al. 2006). Although some of these studies indicated the paraphyly of *Liomys*, all documented the monophyly of species previously allocated to *Heteromys*. Whereas some authors have suggested that all heteromyines should be placed in the genus *Heteromys* to avoid recognition of a paraphyletic *Liomys* (J. C. Hafner et al. 2007), I continue to recognize *Liomys* until conclusive studies with multiple independent data sources (e.g., unlinked nuclear markers) are completed, allowing for a comprehensive reevaluation of the generic-level taxonomy of the subfamily (see R. P. Anderson et al. 2006:1227). Notably, available generic-level names exist for each of the three clades recovered in the subfamily, allowing for the possible designation of three genera, which would acknowledge the substantial morphological and ecological distinctiveness of each clade and maximally promote nomenclatural stability in the subfamily (see R. P. Anderson and Gutiérrez [2009] for discussion of *Schaeferia* Lehmann, described in Lehmann and Schaefer [1979]).

Three unique synapomorphies of the genus *Heteromys* are unreversed in the family Heteromyidae: optic foramen small, with posterior border generally formed by a strong bar of bone; anterior margin of posterior loph of permanent upper premolar [PM4] with a long fold; and permanent lower premolar [pm4] with three or more lophids (R. P. Anderson et al. 2006). In addition, the lateral termi-

nations of the lophs of the upper molars and lophids of the lower molars tend to be smooth in species of *Heteromys*, but generally are pointed in all other heteromyids.

Genus *Heteromys* Desmarest, 1817

Species of *Heteromys* are medium-sized heteromyids (approximately 40–130 g in adults) that constitute an easily recognizable element of the mammalian fauna of South America. Like all members of the superfamily Geomyoidea, they possess external fur-lined cheek pouches. Except for pocket gophers of the family Geomyidae (the sister group to the Heteromyidae), species of *Heteromys* represent the only South American mammals with such cheek pouches. In contrast to the subterranean pocket gophers (which evolved short, broad limbs and large claws for digging), *Heteromys* (like other heteromyids) have small claws and long, thin forelimbs; the hindlimbs are characteristically well developed. In addition to their characteristic cheek pouches, most adult *Heteromys* (like other heteromyines) have spiny dorsal pelage, with dark brown or black spines intermixed with soft and generally slightly paler brown or gray hairs, creating a grizzled effect. However, the dorsal pelage of juveniles of all species and even adults of some populations of some species is soft and more uniform in color. As in the rest of the subfamily, the ventral pelage of individuals of all ages lacks spines and is white, sharply demarcated from the dark pelage of the dorsum. A faint, narrow ventral stripe of dark hairs occurs in some individuals of some species in the midsagittal plane of the throat, chest, and/or abdominal regions. The tail is long—as long as or longer than the length of the head and body. As in other heteromyines, reproductively active adult male *Heteromys* possess extremely large testes, with the scrotal sac extending well posterior and lateral to the base of the tail and creating a distinctive outline in dorsal, ventral, and lateral views.

SYNONYMS:

Mus: Thompson, 1815:161; part (description of *anomalous*); not *Mus* Linnaeus, 1758.

Cricetus: Desmarest, 1817e:180; part (listing of *anomalous*); not *Cricetus* Leske, 1779.

Heteromys Desmarest, 1817e:181; type species *Mus anomalous* Thompson, 1815, by monotypy.

Sacomys F. Cuvier, 1823c:186; type species *Sacomys anthophile* F. Cuvier, 1823d:422, by subsequent designation.

Loncheres: Kuhl, 1820:72; part (listing of *anomala*, presumably a mandatory change of spelling of *anomalous* to match gender of genus).

Dasynotus Wagler, 1830:21; type species *Mus anomalous* Thompson, 1815, by monotypy.

Cricetomys: Schinz, 1845:204; part (listing of *anomalous*); not *Cricetomys* Waterhouse, 1840.

Perognathus: Gray, 1868:202; part (description of *bicolor*); not *Perognathus* Wied-Neuwied, 1839.

Xylomys Merriam, 1902:43; type species *Heteromys (Xylomys) nelsoni* Merriam, 1902, by original designation (subgenus).

REMARKS: F. Cuvier (1823d) described *Sacomys anthophile*, with type locality unknown, based on a single fluid-preserved specimen. This specimen, however, is apparently lost, as no holotype for the species appears in Rode (1945). The same specimen may have been the one in the Muséum National d'Histoire Naturelle in Paris studied by Desmarest (1817e) and considered by him to be conspecific with *Mus anomalous* Thompson. Ellerman (1940:472) stated “the type species of *Sacomys* is presumably unidentifiable.” The illustrations in F. Cuvier (1823d) show dental and external characters that allow placement of the *Sacomys anthophile* in *Heteromys*, but I concur that neither these illustrations nor the extensive textual description are sufficient to associate the specimen with any particular species of the genus. Given the presently available information, I consider *S. anthophile* to be a *nomen dubium*. Note relevant listings by various subsequent authors: *Sacomys anthophilus* Wagler, 1830:22 (incorrect subsequent spelling of *anthophile* F. Cuvier); *H[eteromys]. anthophilus* Alston, 1880b:119 (name combination and incorrect subsequent spelling of *anthophile* F. Cuvier); and *Sacomys anthophilus* Ellerman, 1940:472 (incorrect subsequent spelling of *anthophile* F. Cuvier).

The species-level taxonomy of *Heteromys* remains highly problematic in Mexico and Central America, but South American species have received recent revisionary study. Just over two decades ago, only six (D. F. Williams et al. 1993) or seven (Patton 1993) species were recognized in the genus. However, karyotypic and allozymic studies indicate that the widespread *Heteromys desmarestianus* (currently considered to range from southern Mexico to northwestern Colombia) is composite (Rogers 1989, 1990; Mascarello and Rogers 1988). In addition, morphological studies have revealed several new species, bringing the number of currently recognized species in the genus to 10 (R. P. Anderson and Jarrín 2002; R. P. Anderson 2003; R. P. Anderson and Timm 2006; R. P. Anderson and Gutiérrez 2009). Whereas the species limits of *Heteromys* in Central America remain unclear (in particular in what currently is considered *H. desmarestianus*), the recent revisionary studies of South American species allow the current accounts, which remain subject to evaluation with molecular data.

Even compared with other genera of rodents, specimens from many populations of *Heteromys* are extremely difficult to identify to species, especially when only one or a few specimens are available from a single locality. Vast age-

related cranial variation exists in size and shape, coupled with substantial ontogenetic changes in pelage; hence, age must be taken into account for valid comparisons and reliable identifications (Rogers and Schmidly 1982). Direct comparison with previously identified specimens from large series at single localities (in which age-related variation can be appreciated) is highly desirable and often necessary to ensure correct identification.

KEY TO THE SOUTH AMERICAN SPECIES
OF *HETEROMYS*:

1. Braincase narrow relative to length of skull; interorbital constriction narrow relative to length of skull 2
- 1'. Braincase wide relative to length of skull; interorbital constriction wide relative to length of skull 3
2. Size diminutive (rostral length <13.4 mm in adults); little or no dark coloration present on dorsal and external surfaces of forelimbs. *Heteromys oasicus*
- 2'. Size typical for genus (rostral length >13.4 mm in adults); patch of moderately dark coloration present on dorsal and external surfaces of forelimbs
. *Heteromys anomalus*
3. Rostrum short; dorsal coloration chocolate brown
. *Heteromys desmarestianus crassirostris*
- 3'. Rostrum typical in length for genus; dorsal coloration dark slate gray or black 4
4. Braincase distinctly inflated. *Heteromys australis*
- 4'. Braincase not inflated, or only moderately so 5
5. Zygomatic arches wide and bowed . . . *Heteromys teleus*
- 5'. Zygomatic arches not distinctly bowed, but rather parallel sided, or nearly so *Heteromys catopterus*

Heteromys anomalus (Thompson, 1815)

Caribbean Spiny Pocket Mouse

SYNONYMS:

Mus anomalus Thompson, 1815:161; type locality "Trinidad . . . [near] St. Anne's barracks," Trinidad and Tobago.

Cricetus anomalus: Desmarest, 1817e:180; name combination.

[*Heteromys*] *anomalus*: Desmarest, 1817e:181; name combination and formation as type species by monotypy; first use of current name combination.

Loncheres anomala: Kuhl, 1820:72; name combination.

Heteromys Thompsonii Lesson, 1827:264; type locality "la Trinité," Trinidad, Trinidad and Tobago.

[*Dasynotus*] *anomalus*: Wagler, 1830:21; name combination.
Cr[icetomys]. anomalus: Schinz, 1845:204; name combination.

Heteromys Thomsonii Schinz, 1845:204; incorrect subsequent spelling of *Heteromys thompsonii* Lesson.

Perognathus bicolor Gray, 1868:202; type locality originally given as "Honduras" but subsequently corrected

to "Venezuela" (Alston 1880b:118–119; see also D. F. Williams et al. 1993:102).

Heteromys thompsoni Gray, 1868:203; incorrect subsequent spelling of *Heteromys thompsonii* Lesson.

Heteromys melanoleucus Gray, 1868:204; type locality originally given as "Honduras" but subsequently corrected to "Venezuela" (Alston 1880b:118–119; see also D. F. Williams et al. 1993:102).

Heteromys bicolor: Alston, 1880b:119; name combination.

Heteromys jesupi J. A. Allen, 1899b:201; type locality "near Minca (at an alt. of 1000 ft. [305 m]), Santa Marta District, [Magdalena,] Colombia."

Heteromys anomalus brachialis Osgood, 1912:54; type locality "El Panorama, Rio Aurare [= Río Anaure], eastern shore of Lake Maracaibo, [Zulia,] Venezuela."

Heteromys anomalus jesupi: Osgood, 1912:54; name combination, listed as subspecies.

Heteromys [(*Heteromys*)] *anomalus anomalus*: Ellerman, 1940:475; name combination, listed as nominotypical subspecies.

[*Heteromys* (*Heteromys*)] *melanoleucas* Ellerman, 1940:475; incorrect subsequent spelling of *Heteromys melanoleucus* Gray.

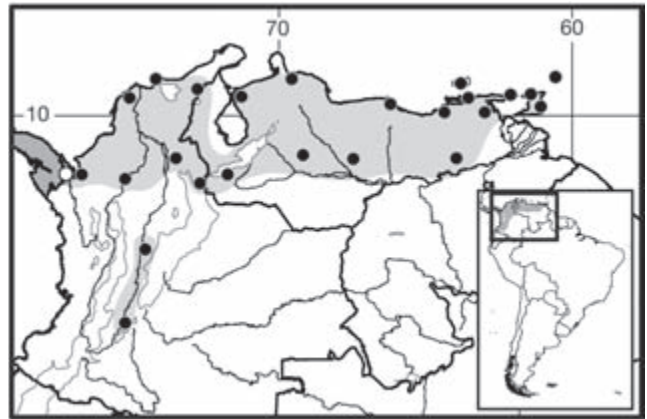
Heteromys (*Heteromys*) *anomalus hershkovitzi*: Hernández-Camacho, 1956:3; type locality "Volcanes, cerca a la cabecera del corregimiento de Córdoba, Municipio de Caparrapí, Departamento de Cundinamarca; vertiente occidental de la Cordillera Oriental, Colombia. Alt. 250 metros." See also R. P. Anderson (1999:618).

DESCRIPTION: Adults with following combination of characters (R. P. Anderson 2003; R. P. Anderson and Gutiérrez 2009; see also R. P. Anderson 1999): Dorsal pelage typically pale brown, strongly grizzled, with thin ochraceous hairs intermixed with spines, but occasionally almost uniformly dark slate gray, nearly uniform to moderately grizzled (in wet lowlands of Zulia state, Venezuela, in some parts of Cordillera de Mérida, in mesic areas of Monagas and Sucre states, Venezuela, and on islands of Trinidad and Tobago); weak patch of dark coloration present on dorsal and external surfaces of forelimbs; ears distinctively rounded, brown to gray and large relative to body size; orange band on flanks absent; plantar surface of hindfeet naked. Skull variable in size geographically, average to large for genus (occipitonasal length 31.1–39.0 mm in adult specimens of age class 4 of Rogers and Schmidly [1982]); rostrum moderately long and moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction narrow; braincase narrow and not inflated; interparietal variable in size and shape; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin

hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone. PM4 with straight, moderately long fold in anterior margin of posterior loph; pm4 with three lophids.

DISTRIBUTION: This species is found in low elevations along Caribbean coast of Colombia and Venezuela (east of Río Atrato), upper Río Magdalena valley of Colombia, gallery forests of *llanos* (savannas) of Venezuela north of Río Orinoco, and up to middle elevations on adjacent slopes of Sierra Nevada de Santa Marta, Cordillera Central (of Colombia; eastern versant only), Cordillera Oriental (of Colombia; western versant only), Serranía de Perijá, Cordillera de Mérida, Cordillera de la Costa (of Venezuela), and other coastal ranges; it also inhabits the Caribbean islands of Margarita, Trinidad, and Tobago; the known elevational range is from near sea level to 2,430 m, but most occurrences are from sea level to approximately 1,600 m (R. P. Anderson and Soriano 1999; R. P. Anderson 2003; R. P. Anderson and Gutiérrez 2009).

SELECTED LOCALITIES (Map 22): **COLOMBIA:** Antioquia, Hacienda Barro, 12 km S of Caucasia (R. P. Anderson 2003), Urabá, Río Currulao (R. P. Anderson 2003); Atlántico, Ciénaga de Guájaro, Sabana Larga (R. P. Anderson 2003); Cundinamarca, Volcanes, Municipio de Caparrapí (type locality of *Heteromys* [*Heteromys*] *anomalous hershkovitzii* Hernández-Camacho); Huila, Camp Coscorón, Hacienda San Diego, 17 km SE of Villavieja (R. P. Anderson 2003); La Guajira, Las Marimondas, Fonseca (R. P. Anderson 2003); Magdalena, Mamatoca (R. P. Anderson 2003); Norte de Santander, Guamalito, near El Carmen (R. P. Anderson 2003), Finca La Palma, Durania (R. P. Anderson 2003). **TRINIDAD AND TOBAGO:** Tobago, Pigeon Peak, Tobago Forest Reserve, 2.5 km SSW of Charlotteville (R. P. Anderson and Gutiérrez 2009); Trinidad, Botanic Gardens, behind St. Anne's barracks (type locality of *Mus anomalous* Thompson), Mayaro (R. P. Anderson and Gutiérrez 2009). **VENEZUELA:** Anzoátegui, Paso Los Cocos, Río Caris, S of El Tigre (R. P. Anderson and Gutiérrez 2009), Pekín Abajo, Río Neverí (R. P. Anderson and Gutiérrez 2009); Falcón, Cerro la Danta, Sierra de San Luis, Parque Nacional J. C. Falcón (R. P. Anderson 2003); Guárico, Fundo Pecuario Masaguaral, 45 km (by road) S of Calabozo (R. P. Anderson and Gutiérrez 2009); Miranda, Estación Experimental Río Negro (R. P. Anderson and Gutiérrez 2009); Monagas, Caripito (R. P. Anderson and Gutiérrez 2009); Nueva Esparta, San Juan, Cerro Copey (R. P. Anderson and Gutiérrez 2009); Portuguesa, Cogollal, near Guanarito (R. P. Anderson 2003); Sucre, población de Macuro, Distrito Valdez (R. P. Anderson and Gutiérrez 2009), entre Cariaco y Chacopata (R. P. Anderson and Gutiérrez 2009); Táchira, Urbante,



Map 22 Selected localities for *Heteromys anomalous* (●) and *Heteromys desmarestianus crassirostris* (○). Range of *H. desmarestianus* in Panama follows Hall (1981). Contour line = 2,000 m.

Río Potosí (R. P. Anderson 2003); Zulia, El Panorama, Río Anaure (type locality of *Heteromys anomalous brachialis* Osgood).

SUBSPECIES: A thorough review of geographic variation in this relatively widespread species has yet to be undertaken, and I do not recognize subspecies at this time (but see D. F. Williams et al. 1993 and Patton 2005a for recognition of four subspecies).

NATURAL HISTORY: *Heteromys anomalous* inhabits both primary and secondary forests, as well as some low-intensity agricultural settings (R. P. Anderson 1999, 2003; R. P. Anderson and Gutiérrez 2009). Most localities are in evergreen and deciduous forests; the available information for records in landscapes dominated by nonforested vegetation indicates that the species is restricted to areas of denser vegetation (e.g., gallery forests) in such situations (Osgood 1912; August 1984; Soriano and Clulow 1988; R. P. Anderson 2003; R. P. Anderson and Gutiérrez 2009). Mark-recapture studies at Bush Bush Forest on Trinidad documented limited movement for individuals of the species (<300 ft [ca. 90 m]; Worth et al. 1968). Eisenberg (1963) reported some behavioral information for the species.

REMARKS: The karyotype is characterized by $2n=60$ and $FN=68$ (Engstrom et al. 1987).

Heteromys australis Thomas, 1901

Southern Spiny Pocket Mouse

SYNONYMS:

Heteromys australis Thomas, 1901c:194; type locality "St. [San] Javier, Lower Cachabi River [Río Cachaví], [Esmeraldas,] N[orthern]. Ecuador. Alt. 20 m."

Heteromys lomitisensis J. A. Allen, 1912:77; type locality "Las Lomitas, Cauca [now Valle del Cauca], Colombia . . . Altitude 5000 feet [1,524 m], west slope of Western Andes."

Heteromys australis consicus Goldman 1913:8; type locality “Cana (altitude 2000 feet [610 m]), [Darién,] Eastern Panama.”

Heteromys australis australis: Goldman, 1913:8; name combination, listed as nominotypical subspecies; see also Goldman (1913:9).

Heteromys australis lomitensis: Goldman, 1913:8; name combination, listed as subspecies; see also Goldman (1913:9).

Heteromys australis pacificus Pearson 1939:4; type locality “Amagal, [Darién,] eastern Panama, altitude 1000 feet [305 m]”.

Heteromys lomitansis Cabrera, 1961:513; incorrect subsequent spelling of *Heteromys lomitensis* J. A. Allen.

DESCRIPTION: Adults characterized by (R. P. Anderson 1999, 2003, R. P. Anderson and Jarrín 2002; see also R. P. Anderson et al. 2006) dorsal coloration of dark slate gray or black, nearly uniform or moderately grizzled with thin ochraceous hairs intermixed with spines; distinctive patch of dark coloration present on dorsal and external surfaces of forelimbs; ears black and small; orange band on flanks absent; plantar surface of hindfeet naked. Skull average to small for genus (occipitonasal length 32.1–36.0 mm in specimens of age class 4 of Rogers and Schmidly [1982] from Ecuador and southwestern Colombia; see also R. P. Anderson [1999]); rostrum unremarkable for genus, but moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming smooth (not stepped) lateral border of rostrum; interorbital constriction wide; braincase wide and distinctly inflated; interparietal wide; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone. PM4 with straight, moderately long fold in anterior margin of posterior loph; pm4 with three lophids.

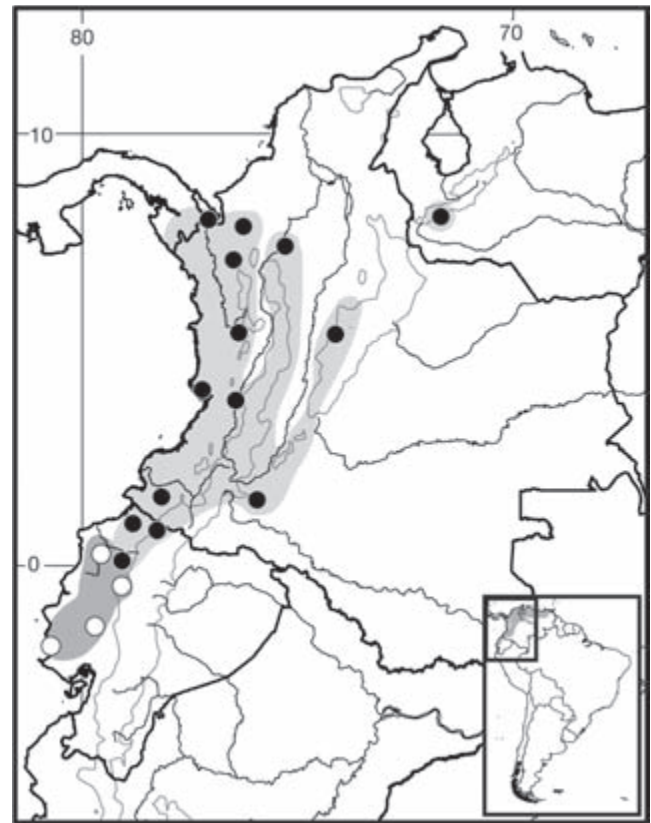
DISTRIBUTION: Low elevations along Pacific coast of northwestern South America, from northwestern Ecuador through western Colombia to eastern Panama, and up to middle and high elevations on adjacent slopes of the Cordillera Occidental (of Ecuador), Cordilleras Occidental and Central (of Colombia), Cordillera Oriental (of Colombia; western versant only), and Cordillera de Mérida (Río Uribante drainage only, apparently disjunct) in western Venezuela. The known elevational range is from near sea level to 2,450 m, but most occurrences are found from sea level to approximately 2,000 m (R. P. Anderson 1999; R. P. Anderson and Jarrín 2002).

SELECTED LOCALITIES (Map 23; from R. P. Anderson 1999, except as noted): COLOMBIA: Antioquia, Alto Bonito, Purí, above Cáceres; Chocó, Bagadó,

Unguía, upper Río Ipetí; Córdoba, Socorré, upper Río Sinú; Cundinamarca, Paime; Huila, near San Adolfo, Río Aguas Claras, Río Suaza; Nariño, Barbaças (R. P. Anderson and Jarrín 2002); Valle del Cauca, Bahía Málaga, Quebrada Valencia, road to Quebrada Alegría, Reserva Forestal Yotoco. ECUADOR: Carchi, El Pailón (Anderson and Jarrín 2002); Esmeraldas, San Javier, Río Cachaví (type locality of *Heteromys australis* Thomas); Pichincha, Cooperativa Salcedo Lindo, on road from Pedro Vicente Maldonado to Encampamento de CODESA (R. P. Anderson and Jarrín 2002). VENEZUELA: Táchira, Presa La Honda, 10 km SSE of Pregonero (R. P. Anderson 2003).

SUBSPECIES: A thorough review of geographic variation in this relatively widespread species has yet to be undertaken, and I do not recognize subspecies (but see D. F. Williams et al. 1993 and Patton 2005a for recognition of three subspecies).

NATURAL HISTORY: *Heteromys australis* inhabits very wet, unseasonal evergreen forests, but very little additional information regarding its natural history is available (R. P. Anderson 1999; R. P. Anderson and Jarrín 2002).



Map 23 Selected localities for *Heteromys australis* (●) and *Heteromys teleus* (○). The disjunct locality of *H. australis* in the Cordillera de Mérida of Venezuela is mapped separately from the remainder of the species' distribution; its range in Panama follows Hall (1981). Contour line = 2,000 m.

REMARKS: The karyotype is unknown. Populations in central Colombia may be specifically distinct from *H. australis* (R. P. Anderson 1999:620).

Heteromys catopterus R. P. Anderson and Gutiérrez, 2009

Overlook Spiny Pocket Mouse

SYNONYMS:

Heteromys anomalus: Tate, 1947:66; part; first name combination applied.

Heteromys catopterus R. P. Anderson and Gutiérrez, 2009:40; type locality "Venezuela: Aragua: Rancho Grande, near Biological Station, 13 km NW Maracay, at 3576 ft [1,090 m]."

DESCRIPTION: Adults with following combination of characters (R. P. Anderson and Gutiérrez 2009): dorsal coloration dark slate gray or black, moderately grizzled with thin ochraceous hairs intermixed with spines; distinctive patch of dark coloration present on dorsal and external surfaces of forelimbs; ears dark gray to black and medium in size; orange band on flanks absent; plantar surface of hindfeet naked. Skull average to large for genus (occipito-nasal length 34.7–38.7 mm in adult specimens of age class 4 of Rogers and Schmidly [1982]); rostrum long and wide, only slightly to moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction wide; braincase wide and moderately inflated; interparietal wide; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone. PM4 with straight, moderately long fold in anterior margin of posterior loph; pm4 with three lophids.

DISTRIBUTION: Middle-to-high elevations of the Cordillera de la Costa of Venezuela. The known elevational range is from 350 to 2,425 m, but most records are above approximately 700 m (R. P. Anderson and Gutiérrez 2009).

SELECTED LOCALITIES (Map 24; from R. P. Anderson and Gutiérrez 2009). VENEZUELA: Aragua, Campamento Rafael Rangel, Loma de Hierro [= Minas de Niquel], 10 km (by road) WNW [NNE] of Tiara; Carabobo, Campamento La Justa, Río Morón; Miranda, 25 km (by road) N of Altagracia de Orituco, Hacienda Las Planadas; Monagas, 2 km N and 4 km W of Caripe, near San Agustín.

SUBSPECIES: *Heteromys catopterus* is monotypic.

NATURAL HISTORY: *Heteromys catopterus* inhabits wet montane forests, particularly cloud forests with many palms, and has been collected in both primary and second-



Map 24 Selected localities for *Heteromys catopterus* (●) (note disjunct range, with absence from the lowlands of the Depresión de Unare on the coast) and *Heteromys oasicus* (○). Contour line=2,000 m.

ary forests (R. P. Anderson and Gutiérrez 2009). Rood (1963) and Rood and Test (1968) provided substantial information regarding the reproduction, development, diet, and behavior for the species.

REMARKS: The karyotype is characterized by $2n=60$ and $FN=72$ (Schmid et al. 1992). However, the FN reported by those authors included the four arms of the female sex chromosomes; thus, the autosomal FN is actually 68 (R. P. Anderson and Gutiérrez 2009). The Y chromosome of this species shows exceptional quinacrine-positive heterochromatin, indicating a preponderance of AT-rich sequences (Schmid et al. 1992).

Heteromys desmarestianus Gray, 1868

Desmarest's Spiny Pocket Mouse

SYNONYMS: [Synonymy for forms from Mexico and elsewhere in Central America not included; see Hall 1981; D. F. Williams et al. 1983.]

Heteromys desmarestianus Gray, 1868:204; type locality "Coban [Cobán]," Departamento de Alta Verapaz, Guatemala.

Heteromys crassirostris Goldman, 1912b:10; type locality "near head of Río Limón [Río Limón] (altitude 5,000 feet [1,524 m]), Mount Pirri [= Cerro Pirre], [Darién], eastern Panama."

Heteromys desmarestianus crassirostris: Goldman, 1920:115; name combination, listed as valid subspecies; see also Goldman (1920:117–118).

Heteromys d[esmarestianus], *acutirostris* R. P. Anderson, 1999:623; incorrect subsequent spelling of *Heteromys crassirostris* Goldman; editor's error.

DESCRIPTION: (For *H. desmarestianus crassirostris*, see Remarks.) Adults with following combination of characters (R. P. Anderson 1999; see also R. P. Anderson and Timm 2006 and R. P. Anderson et al. 2006): dorsal pelage chocolate brown, only moderately grizzled with thin ochraceous hairs intermixed among spines; distinctive patch of dark coloration present on dorsal and external surfaces of forelimbs; ears small; orange band on flanks absent; plantar surface of hindfeet naked. Skull small for genus (occipito-nasal length 32.2–35.1 mm in adult specimens of age classes 4 and 5 of Rogers and Schmidly [1982; published data for age class 4 not available]); rostrum distinctively short, wide, and strongly tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming smooth (not stepped) lateral border of rostrum; interorbital constriction wide; braincase wide and moderately inflated; interparietal moderately wide; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen small, with posterior margin formed by strong bar of bone. PM4 with bent, extremely long fold in anterior margin of posterior loph; pm4 with three lophids.

DISTRIBUTION: Definitive distribution of this species of the *H. desmarestianus* species complex is only confirmed for extreme northwestern Colombia and eastern Panama along the Serranía del Darién and associated mountain chains (R. P. Anderson 1999; R. P. Anderson et al. 2006).

SELECTED LOCALITIES (Map 22, in South America): COLOMBIA: Chocó, Alto de Barrigonal, Serranía del Darién (R. P. Anderson 1999).

SUBSPECIES: *Heteromys desmarestianus*, as currently conceived, is polytypic, with 12 subspecies recognized (D. F. Williams et al. 1993; Patton 2005a). As presently understood, only *H. d. crassirostris* Goldman extends into South America (see Remarks).

NATURAL HISTORY: This form is known from cloud forests along the Colombian-Panamanian border, where it is locally common (R. P. Anderson 1999). The contents of cheek pouches have included a variety of seeds, nuts, and other items (R. P. Anderson 1999).

REMARKS: Morphological, karyological, and allozymic data indicate that, as currently conceived, *Heteromys desmarestianus* represents a complex of several species (Mascarello and Rogers 1988; Rogers 1989, 1990; R. P. Anderson and Timm 2006; R. P. Anderson et al. 2006). Detailed specimen-based studies of alpha-level taxonomy are needed to elucidate the species in this complex, and current knowledge does not permit definitive conclusions

regarding the valid name for the species present in extreme northwestern Colombia. These populations are provisionally referred to here as *H. d. crassirostris* (following R. P. Anderson 1999; R. P. Anderson et al. 2006). A karyotype for these populations is unknown.

Heteromys oasicus R. P. Anderson, 2003

Paraguana Spiny Pocket Mouse

SYNONYMS:

Heteromys anomalus: Bisbal-E., 1990:180; first name combination applied.

Heteromys oasicus R. P. Anderson, 2003:9; type locality "Venezuela: Estado Falcón: 49 km N, 32 km W of Coro, Cerro Santa Ana, at 550 m."

DESCRIPTION: Adults have following combination of characters (R. P. Anderson 2003). Dorsal pelage very pale brown, strongly grizzled with thin ochraceous hairs intermixed with spines; little or no dark coloration on dorsal and external surfaces of forelimbs; ears pale brown and large relative to body size; orange band on flanks absent; plantar surface of hindfeet naked. Skull diminutive for genus (occipito-nasal length 29.7–31.2 mm in adult specimens of age class 4 of Rogers and Schmidly [1982]); rostrum short and strongly tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction narrow; braincase narrow and not inflated; interparietal moderately wide and rounded laterally; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone. PM4 with straight, moderately long fold in anterior margin of posterior loph; pm4 with three lophids.

DISTRIBUTION: Low-to-middle elevations of Cerro Santa Ana and Fila de Monte Cano on the Península de Paraguana in northwestern Venezuela; known elevational range from 90 to 700 m (R. P. Anderson et al. 2012).

SELECTED LOCALITIES (Map 24): VENEZUELA: Falcón, 49 km N and 32 km W of Coro, Cerro Santa Ana (type locality of *Heteromys oasicus* R. P. Anderson).

SUBSPECIES: *Heteromys oasicus* is monotypic.

NATURAL HISTORY: *Heteromys oasicus* inhabits small, isolated areas of forests, especially evergreen vegetation on the upper slopes of Cerro Santa Ana, but it also has been captured in riparian vegetation at lower elevations (i.e., on the lower slopes of Cerro Santa Ana and along the Fila de Monte Cano; R. P. Anderson 2003).

REMARKS: The karyotype is unknown.

Heteromys teleus R. P. Anderson and Jarrín, 2002

Ecuadorian Spiny Pocket Mouse

SYNONYMS:

Heteromys australis: Albuja, 1992:125; first name combination applied.

Heteromys teleus R. P. Anderson and Jarrín, 2002:6; type locality “Ecuador: Provincia Guayas [now Santa Elena]: Cerro Manglar Alto, western slope . . . 2000 ft [610 m].”

DESCRIPTION: Adults with following combination of characters (R. P. Anderson and Jarrín 2002; see also R. P. Anderson et al. 2006): dorsal coloration dark slate gray or black, nearly uniform or moderately grizzled with thin ochraceous hairs intermixed with spines; distinctive patch of dark coloration on dorsal and external surfaces of forelimbs; ears black and small to medium in size; orange band on flanks absent; plantar surface of hindfeet naked. Skull size average to large for genus (occipitonasal length 35.5–38.3 mm in adult specimens of age class 4 of Rogers and Schmidly [1982]); rostrum extremely wide and only slightly to moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming smooth (not stepped) lateral border of rostrum; interorbital constriction moderately wide; braincase moderately wide and not inflated; interparietal narrow and rounded laterally; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone. PM4 with straight, moderately long fold in anterior margin of posterior loph; pm4 with three lophids.

DISTRIBUTION: Low elevations along the Pacific coast of central-western Ecuador, and up to middle elevations on adjacent slopes of Cordillera Occidental and Cordillera de Chongón-Colonche of Ecuador. The known elevational range is from near sea level to 2,000 m, but most records are from sea level to approximately 600 m (R. P. Anderson and Jarrín 2002).

SELECTED LOCALITIES (Map 23; from R. P. Anderson and Jarrín 2002): ECUADOR: Cotopaxi, San Francisco de las Pampas, Reserva Bosque Nublado Otonga; Esmeraldas, Quinindé; Los Ríos, Estación Biológica Pedro Franco Dávila, Jauneche; Santa Elena, Cerro Manglar Alto, western slope (type locality of *Heteromys teleus* R. P. Anderson and Jarrín).

SUBSPECIES: *Heteromys teleus* is monotypic.

NATURAL HISTORY: *Heteromys teleus* inhabits evergreen but seasonal forests and is tolerant of moderate levels of disturbance (R. P. Anderson and Jarrín 2002). In the region near the type locality, almost all specimens were captured on the banks of small streams (R. P. Anderson and Jarrín 2002). R. P. Anderson and Martínez-Meyer (2004) provided an estimate of the species’ potential geographic distribution and a preliminary conservation assessment.

REMARKS: The karyotype is unknown.

Suborder Myomorpha Brants, 1855

James L. Patton

Infraorder Myodonta Schaub, in Grassé and Dekeyser, 1955

Superfamily Muroidea Illiger, 1811

Family Cricetidae G. Fischer, 1817

The muroid rodents of the suborder Myomorpha comprise three subfamilies of the Cricetidae in South America. Two of these, the Neotominae and Tylomyinae, are North or Middle American lineages of which a single genus of the latter and two of the former extend into northwestern South America. The third, the Sigmodontinae, are highly diverse and largely autochthonous to that continent, with a few members extending north into Middle America and reaching a northern limit in the northeastern United States. These three groups, together with the Holarctic Arvicolinae and Old World Cricetinae, are currently included in the Cricetidae (e.g., Musser and Carleton 2005). Initial molecular analyses (e.g., Jansa and Weksler 2004; Stepan, Adkins, and Anderson 2004) failed to recover robust phylogenetic relationships among the three subfamilies that occur in South America. However, three recent taxon and gene-expanded studies (Parada et al. 2013; Schenk et al. 2013; J. F. Vilela et al. 2013) supported a sister relationship between the Tylomyinae and Sigmodontinae; the latter authors posited the split between the two subfamilies at about 18 mya based on a time-calibrated ultrametric tree analysis.

Musser and Carleton (2005) detailed the long and tortuous history of the concept of the Muroidea, answering the question these two authors had posed in 1984 about the number of families to recognize and the family-group ranks for those lineages recognized in the New World, specifically South America. Although refinements to what is known of phyletic relationships and group membership will continue, particularly with the future expansion of molecular analyses, the three subfamilies of Cricetidae now recognized as part of the native fauna of South America will likely remain stable into the foreseeable future (see Schenk et al. 2013).

The Sigmodontinae comprise the vast majority of cricetid rodents in South America, representing a large radiation (approximately 84 genera and nearly 380 species), with representatives occupying virtually all habitats from sea level to the high Andes, and from evergreen rainforests of the Amazon to some of the world’s most xeric communities along the Pacific coast from central Peru to northern Chile. Only single species of *Reithrodontomys* and of *Isthmomys* of the otherwise highly diverse and mostly North