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A New Montane Species of Spiny Pocket Mouse (Rodentia: Heteromyidae: *Heteromys*) from Northwestern Costa Rica

ROBERT P. ANDERSON,[1,2] AND ROBERT M. TIMM[3]

ABSTRACT

Recent taxonomic works have recognized only two species of spiny pocket mice of the genus *Heteromys* (Rodentia: Heteromyidae) from Costa Rica. Within Costa Rica, the widespread *H. desmarestianus* is considered to occur throughout the wet Caribbean lowlands, as well as at middle and high elevations on the Caribbean and Pacific slopes of the country's main montane systems. In contrast, *H. oresterus* is known from only a few localities at high elevations in the western portion of the Cordillera de Talamanca in central Costa Rica. Our morphological and morphometric analyses of specimens from northwestern Costa Rica reveal the presence of an undescribed species of the genus, which we describe as *Heteromys nubicolens*. This new species ranges from 750 to 1840 m in elevation in the Cordillera de Tilarán and Cordillera de Guanacaste. *Heteromys desmarestianus* is found in the surrounding mesic lowlands and foothills. Externally, both species possess dark brown dorsal pelage, but *H. nubicolens* differs by overall larger size and by distinctive cranial proportions. In most cranial measurements, *H. nubicolens* is larger than *H. desmarestianus*; however, *H. desmarestianus* has a wider interorbital region and a wider braincase. Known populations of *H. nubicolens* occur in three highland areas (Monteverde, Volcán Rincón de la Vieja–Volcán Santa María, and Cerro Cacao), but populations in these areas are probably disjunct, being separated by intervening lowlands. *Heteromys nubicolens* is likely widespread throughout the Cordillera de Tilarán and Cordillera de Guanacaste, but its presence in other areas of the country is unlikely. Even after recognizing *H. nubicolens* as distinct from *H. desmarestianus*, morphological, karyological, and genetic data indicate that *H. desmarestianus* represents a species complex. Further research is therefore necessary to evaluate the taxonomic status of this species complex in other regions of the country and other parts of its widespread geographic distribution.

RESUMEN

Recientes trabajos taxonómicos han considerado que sólo dos especies de ratones de abazones (= ratón bolsero, raton bolsón, ratón mochilero) del género *Heteromys* (Rodentia: Heteromyidae)

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habitan en Costa Rica. *Heteromys desmarestianus*, con una amplia distribución general, habita en ese país en las tierras bajas húmedas del Caribe, así como también en las estribaciones caribeñas y pacíficas de las principales cadenas montañosas, en altitudes medias y elevadas. Por el contrario, *H. oresterus* se conoce sólo de unas pocas localidades de alta montaña en la parte occidental de la Cordillera de Talamanca, en la región central de Costa Rica. Nuestros análisis morfológicos y morfométricos de ejemplares provenientes del noroccidente costarricense revelan la presencia de una especie no descrita del género, la cual describimos acá como *Heteromys nubicolens*. Esta nueva especie habita entre los 750 y los 1840 m de altitud en la Cordillera de Tilarán y la Cordillera de Guanacaste. *Heteromys desmarestianus* se encuentra en el piedemonte y en las tierras bajas húmedas adyacentes a estas cordilleras, rodeando la distribución de *H. nubicolens*. Externamente ambas especies poseen un pelaje dorsal de coloración parda oscura, pero *H. nubicolens* se caracteriza por tener en general un mayor tamaño corporal y proporciones craneanas distintivas. En la mayoría de las medidas craneanas, *H. nubicolens* posee un mayor tamaño que *H. desmarestianus*; sin embargo, *H. desmarestianus* tiene una mayor anchura de la región interorbital y de la caja craneana. Las poblaciones conocidas de *H. nubicolens* se encuentran en tres áreas de alta montaña (Monteverde, el Volcán Rincón de la Vieja–Volcán Santa María y el Cerro Cacao), pero estas poblaciones probablemente poseen distribuciones disyuntas, estando separadas por las tierras bajas que se interponen entre ellas. Es probable que *H. nubicolens* tenga una amplia distribución en la Cordillera de Tilarán y la Cordillera de Guanacaste, pero su presencia es poco probable en otras regiones del país. Incluso con el reconocimiento de *H. nubicolens* como una especie diferente a *H. desmarestianus*, datos morfológicos, cariológicos y genéticos indican que *H. desmarestianus* constituye un complejo de especies. Por lo tanto, se necesitan estudios adicionales para evaluar la taxonomía de este complejo de especies en otras partes del país y en otras regiones de su amplia distribución geográfica.

INTRODUCTION

Although Costa Rica encompasses an area of only ca. 51,000 km^2, the region's complex geological history and highly variable topography and climate have contributed to a diverse fauna and flora (Janzen, 1983; McPherson 1985, 1986; Wilson et al., 2002). This portion of the Central American isthmus was formed by an extremely complex series of events related to the subduction of the Cocos Plate under the Caribbean Plate (Coates and Obando, 1996; Denyer et al., 2000; Montero-P., 2000). Today, four major mountain ranges exist in Costa Rica, each oriented diagonally from southeast to northwest (fig. 1); these ranges vary greatly in origin and age (Castillo-M., 1984; Bergoeing, 1998; Alvarado et al., 2000; Kussmaul, 2000; Salazar-Mondragón, 2000). The Cordillera de Talamanca represents the highest and most massive montane system in southern Central America. Formed primarily during the Tertiary, this range of mixed geological origin extends from western Panama to central Costa Rica, with many peaks reaching more than 3000 m in elevation. The Cordillera Central of Costa Rica is a younger (Quaternary) volcanic range that lies to the north of the Cordillera de Talamanca. Nearly continuous at an elevation of 1500 m, it contains several peaks higher than 2500 m. A broad connection, the Valle Central (or Meseta Central), joins the Cordillera Central and the northwestern portion of the Cordillera de Talamanca at elevations of ca. 1000–1500 m. To the northwest of the Cordillera Central, an older range of lower (<2000 m) Tertiary volcanic peaks and ridges forms the Cordillera de Tilarán, which is continuous at an elevation of ca. 1200 m. Finally, the Cordillera de Guanacaste represents the northernmost mountain range in the country. Similar in origin to the Cordillera Central, it runs from the Cordillera de Tilarán to near the Nicaraguan border and is comprised of a series of isolated Quaternary volcanoes, most of which reach 1500–2000 m. Low passes between most of the volcanoes of the Cordillera de Guanacaste connect the Caribbean and Pacific lowlands at elevations of 500–700 m. To the north of this range lie the expansive Nicaraguan lowlands.

SPINY POCKET MICE

The rodent family Heteromyidae is comprised of three subfamilies: Heteromyinae

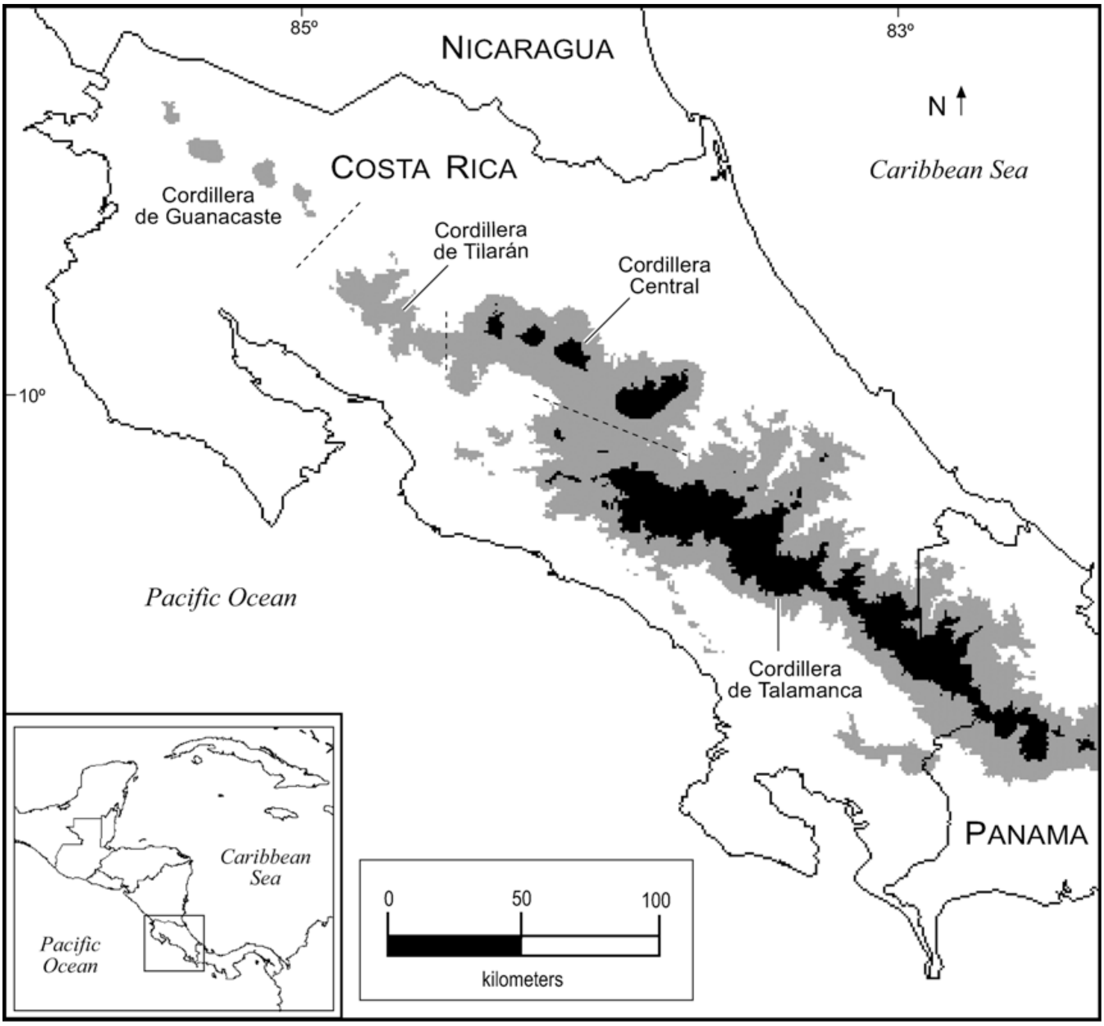

Fig. 1. Map of Costa Rica and adjacent regions of Nicaragua and Panama, showing the position of major mountain ranges. Gray shading denotes regions higher than 1000 m in elevation, and areas shown in black lie above 2000 m.

(spiny pocket mice), Dipodomyinae (kangaroo rats and kangaroo mice), and Perognathinae (silky pocket mice). Heteromyines represent a well-defined monophyletic group distinct from either of the two other living subfamilies (Hafner, 1981; Hafner and Hafner, 1983; Wahlert, 1991; see also Ryan, 1989: 94–98; Brylski, 1990). Two extant genera, *Heteromys* and *Liomys*, are recognized in the Heteromyinae and can be distinguished from each other by a number of morphological characters (Anderson, 2003b). Species of *Liomys* inhabit deciduous forests and other semiarid tropical and subtropical habitats from northern Mexico and southern Texas to Panama (Genoways, 1973; Morales and Engstrom, 1989; Rogers and Engstrom, 1992; Williams et al., 1993). In contrast, species of *Heteromys* inhabit wetter (typically evergreen) forests from southern Mexico to western Ecuador (Williams et al., 1993; Anderson, 1999; Anderson and Jarrín-V., 2002; Anderson, 2003b).

Present taxonomy recognizes eight species of *Heteromys*, including two recently described from northern South America

(Williams et al., 1993; Anderson and Jarrín-V., 2002; Anderson, 2003b; but see Patton, 1993). Of these, only three species are known from southern Central America (Nicaragua, Costa Rica, and Panama): *H. desmarestianus*, *H. oresterus*, and *H. australis* (Patton, 1993; Williams et al., 1993; Reid, 1997; Wilson et al., 2002; see also Goodwin, 1946; Wainwright, 2002). As currently conceived, the widespread *H. desmarestianus* ranges from southern Mexico (Estado de Veracruz) to northwestern Colombia in a wide variety of both lowland and montane habitats. In contrast, *H. oresterus* is endemic to the Cordillera de Talamanca in central Costa Rica. Finally, the primarily South American species *H. australis* shows a marginal distribution in extreme eastern Panama (Anderson, 1999).

Although *Heteromys desmarestianus* is often an abundant member of small mammal communities in Mexico and Central America and has been well studied ecologically at a few classical localities (e.g., Fleming, 1983; Timm et al., 1989; Sánchez-Cordero, 1993), several studies have indicated that it represents a complex of externally similar species. Across the range of the species complex, considerable variation exists in karyotypes and allozymes (Mascarello and Rogers, 1988; Rogers, 1989, 1990) and in cranial morphology (Rogers, 1986). Recent fieldwork by several researchers in the Cordillera de Tilarán and Cordillera de Guanacaste in northwestern Costa Rica has led to new collections of a distinctive species of *Heteromys*. We herein undertake a revision of *Heteromys* in northwestern Costa Rica, describe a species new to science, provide detailed morphological comparisons between it and adjacent populations of *H. desmarestianus*, and summarize the natural history and biogeographic information available for the new species. This work represents a step toward characterizing the morphology and distributions of *H. desmarestianus* and the species currently confused with it. We hope that it will facilitate future studies by other researchers, leading to a more complete taxonomic understanding of these common rodents so characteristic of rainforest habitats in the northern Neotropics.

MATERIALS AND METHODS

Museum Specimens

We examined 401 specimens of *Heteromys* from the principal study area of northwestern Costa Rica, representing all known to us from that region (appendix 1). For the purposes of this paper, we define northwestern Costa Rica as those areas of the country northwest of the depression that separates the Cordillera de Tilarán from the Cordillera Central,[4] and north of the crest of the Cordillera Central (fig. 1). This study region includes the totality of the Provincia de Guanacaste, large portions of the Provincia de Alajuela and Provincia de Heredia, and the extreme northern part of the Provincia de Puntarenas. Although our main interest was in comparing the distinctive populations of *Heteromys* found at upper elevations of the Cordillera de Tilarán and Cordillera de Guanacaste with populations of *H. desmarestianus* present in the immediately adjacent foothills and lowlands, delimitation of the present principal study area also allowed us to make comparisons with specimens from highland regions in the Cordillera Central and with a much larger sample of *H. desmarestianus* from the Caribbean lowlands.

We also examined critical specimens from other regions (appendix 2). These included all Costa Rican and Panamanian voucher specimens from karyological and genetic studies (Mascarello and Rogers 1988; Rogers 1989, 1990). Furthermore, we examined representative samples of all currently recognized species of *Heteromys*, including almost all holotypes and lectotypes representing nominal taxa currently referred to the genus. The only holotype or lectotype in the genus that we did not examine is that of *H. desmarestianus psakastus*; in lieu of the holotype, we examined eight paratypes. Apparently, no holotype exists for *H. thompsonii*, a name that Lesson (1827) clearly used to refer to the spiny pocket mouse from Trinidad named by Thompson

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[4] The southern slope of the division between the Cordillera de Tilarán and the Cordillera Central is marked approximately by the course of the Río Barranca, although the hills of the Montes del Aguacate to the southeast of that river (near San Ramón) are similar to the Cordillera de Tilarán in geological origin (Bergoeing, 1998; Kussmaul, 2000).

(1815) as *Mus anomalus*, now referred to as *H. anomalus*. In considerations of species boundaries, we apply morphological and (when available) karyotypic and/or genetic data to allow evaluation under the evolutionary species concept (Wiley, 1978).

Localities and specimens examined from northwestern Costa Rica are detailed in the Gazetteer (appendix 1), and other specimens examined are listed separately (appendix 2). Locality information not provided by the collector appears in brackets and, where applicable, is followed by the source. Where the original elevation was reported in feet, we provide that datum as well as the metric equivalent to the nearest whole number. Specimens examined are housed in the following museum collections (where applicable, abbreviations follow Hafner et al., 1997—except for UCR, see Savage, 2002). An asterisk denotes museums with material from northwestern Costa Rica.

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia
BM(NH)	Natural History Museum, London [formerly British Museum (Natural History)]
EBRG	Museo de la Estación Biológica de Rancho Grande, Maracay, Aragua
FMNH*	Field Museum, Chicago [formerly Field Museum of Natural History]
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá
KU*	University of Kansas Natural History Museum, Lawrence
LACM*	Natural History Museum of Los Angeles County, Los Angeles
LSUMZ*	Louisiana State University Museum of Natural Science, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNCR*	Museo Nacional de Costa Rica, San José
MVZ*	Museum of Vertebrate Zoology, University of California, Berkeley
ROM*	Royal Ontario Museum, Toronto
UCR*	Museo de Zoología, Universidad de Costa Rica, San José
UMMZ*	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum of Natural History, Washington, DC

We examined external and cranial morphological characters, making comparisons among specimens of approximately the same age. Cranial nomenclature follows Wahlert (1985), Anderson (1999, 2003b), and Anderson and Jarrín-V. (2002). Specimens were assigned to the age classes of Rogers and Schmidly (1982) based on patterns of tooth eruption, toothwear, and molt. Age classes 1–3 represent juveniles and subadults; classes 4–6 are progressively older adults. Age classes do not constitute a continuous variable (such as absolute age), but rather are categories roughly corresponding to relative age within population samples (Voss et al., 1990).

Measurements

Standard cranial measurements for *Heteromys* (fig. 2) follow Anderson and Jarrín-V. (2002) and were taken to the nearest 0.01 mm with digital calipers. We measured all adult specimens of *Heteromys* in age class 4 with intact skulls from northwestern Costa Rica, as well as from all available samples of *H. oresterus*. External measurements and mass were copied from specimen tags and, when necessary, from primary field notes.

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

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

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

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

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

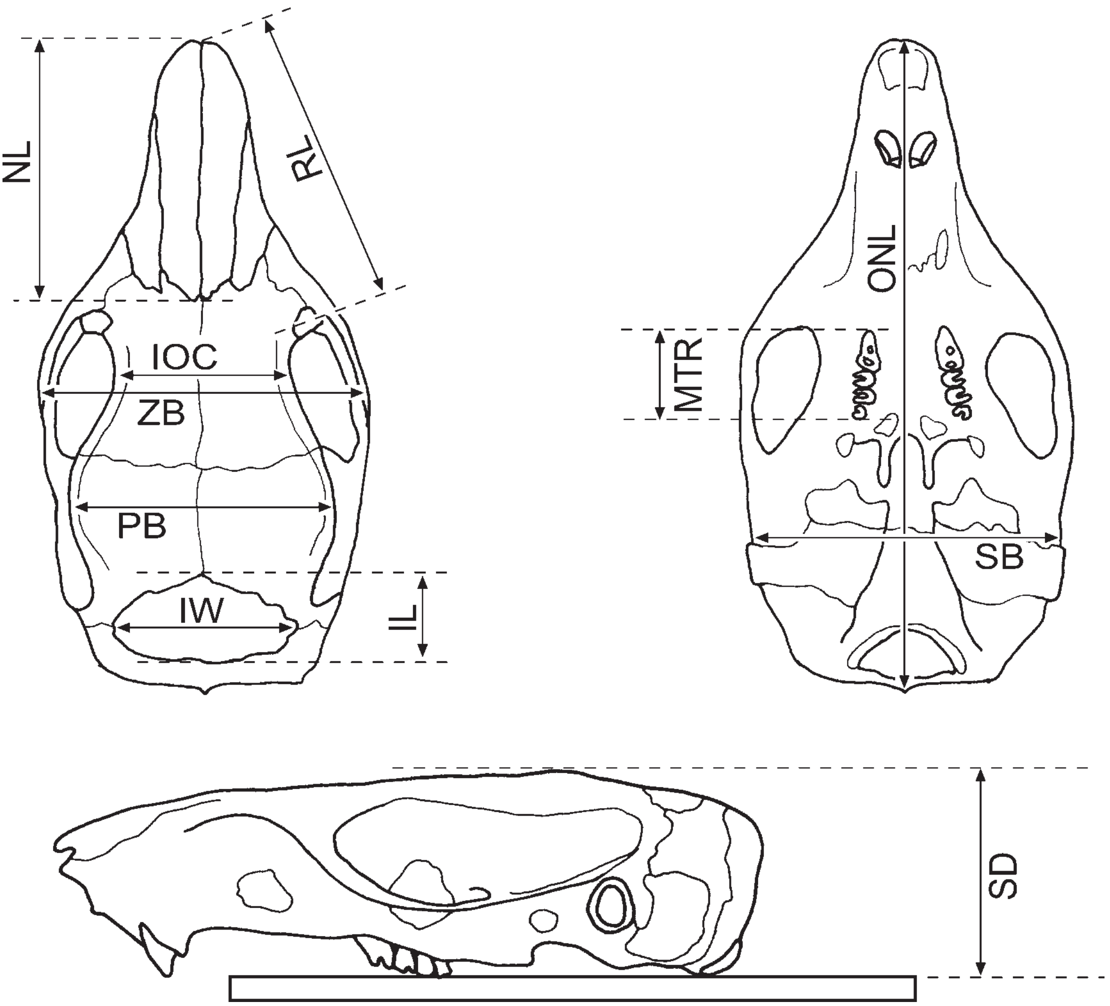

Fig. 2. Dorsal, ventral, and lateral views of a cranium of *Heteromys* showing the methods for taking measurements. Abbreviations and measurements are defined in Materials and Methods.

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

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

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

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

Parietal breadth (PB): greatest width across parietal crests at right angle to longitudinal axis of cranium.

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

Statistics

Specimens in age class 4 (the most abundant adult age class) were used for all quantitative comparisons. Statistical analyses were performed in Minitab (1998; release 12.1), and probabilities were compared to $\alpha = 0.05$ for hypothesis testing. Material from northwestern Costa Rica was used for the primary analyses detailed here. Using species assignments based on our qualitative morphological examinations, we calculated descriptive statistics for standard external measurements, mass, cranial measurements, and three derived ratios (tail length/head-and-body length; least interorbital constriction/occipitonasal length; and parietal breadth/occipitonasal length). For these analyses, all localities for each species were pooled because sample sizes were too small at most individual sites. Additionally, we conducted a series of two-tailed *t*-tests comparing means of the two species for each measurement or ratio.

We then conducted analyses of three geographic samples in northwestern Costa Rica with relatively large sample sizes. In two cases, nearby localities were pooled to create the samples. La Selva (localities 18, 19; appendix 1), Cerro Cacao (locality 28), and Monteverde (localities 30–32; all on the Pacific slope or crest of the Cordillera de Tilarán) constituted these samples. First, we calculated the same descriptive statistics mentioned above. Then, to test for morphological differentiation between highland samples from the Cordillera de Tilarán and the Cordillera de Guanacaste, we conducted a series of two-tailed *t*-tests comparing means of the samples from Cerro Cacao and Monteverde for those measurements and ratios.

We also compared the highland species from northwestern Costa Rica with *Heteromys oresterus* (known only from the Cordillera de Talamanca) using the measurements and ratios mentioned above. To do so, we first calculated standard descriptive statistics for specimens from the type locality of *H. oresterus* (El Copey de Dota). Next, we calculated descriptive statistics for all individuals (of age class 4) that we consider to be *H. oresterus* (appendix 2). We then conducted a series of two-tailed *t*-tests comparing means of *H. oresterus* with those of the montane species from northwestern Costa Rica.

Finally, we conducted a principal components analysis (PCA) of specimens from northwestern Costa Rica, based on the variance-covariance matrix of $\log_e$-transformed cranial measurements. We interpreted the multivariate axes by examination of loadings and of coefficients (elements) of the unit eigenvector. Loadings are Pearson product-moment correlation coefficients between specimen scores on each axis and the $\log_e$-transformed variables.

SYSTEMATICS

A New Species of *Heteromys* from Northwestern Costa Rica

Our analyses indicate that two species of *Heteromys* are present in northwestern Costa Rica. In this region, *Heteromys desmarestianus* is widely distributed in mesic areas from low elevations to ca. 1000 m in the Cordillera de Tilarán and Cordillera de Guanacaste, but it ascends to more than 2000 m in the Cordillera Central. The other species is restricted to middle and high elevations of the Cordillera de Tilarán and Cordillera de Guanacaste (750–1840 m). It displays cranial proportions and measurements distinct from those of *H. desmarestianus*, as well as differences from all other recognized species of the genus. As no available name exists for this species, we describe it as:

Heteromys nubicolens, new species

Cloud-dwelling Spiny Pocket Mouse

Figures 3, 5, 6, 7

Holotype: KU 159025, nulliparous adult female; skin, skull, and postcranial skeleton in excellent condition; plus frozen tissues originally preserved in 95% ethanol (fig. 3). Collected on 16 October 2000 from COSTA RICA: Puntarenas: Monteverde, Monteverde Cloud Forest Reserve, Investigator's Trail, 10°18′N, 84°48′W, at 1550 m elevation by Robert M. Timm and Christy M. McCain; original number RMT 4468.

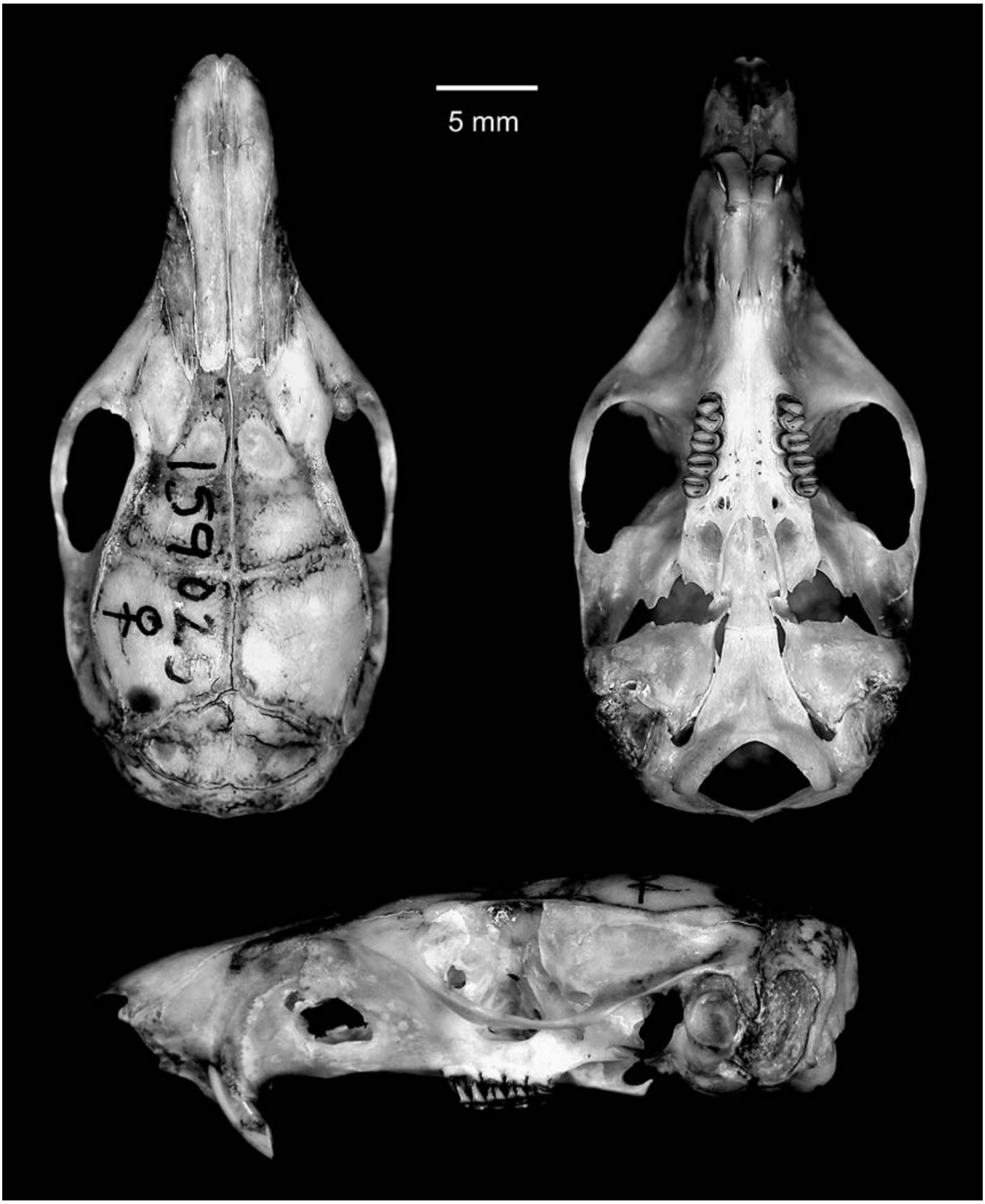

Fig. 3. Dorsal, ventral, and lateral views of the cranium of the holotype of *Heteromys nubicolens* (KU 159025), an adult female in age class 4. See appendix 1 for full provenience.

PARATYPES: We designate as paratypes the following 24 specimens (adults in age classes 4–6; skins and skulls in good condition) from the Pacific slope or crest of the Cordillera de Tilarán in the Monteverde region, and housed in a variety of museum collections (appendix 1): COSTA RICA: PUNTARENAS: Monteverde, 1450 m, ROM 97307; Monteverde, Arthur Rockwell's cafetales, 1400 m, UMMZ 115419, 115420; Monteverde, Cerro Amigos, 1790 m, KU 142057; Monteverde, Hoge woods, 1420 m, LACM 64867; Monteverde, John Campbell's woods, 1520–1580 m, FMNH 128417, 128419, 128420, 128423, 128425; KU 142791; LACM 64863, 64865; MVZ 161224, 161225; Monteverde, Monteverde Cloud Forest Reserve, Investigator's Trail, 1550 m, KU 159022–159024, 159026, 159027, 159029; MNCR 1336; Monteverde, Quebrada Quecha, KU 143337; Monteverde, Stella Wallace's house, KU 143339.

ETYMOLOGY: The adjective *nubicolens*, or "cloud-dwelling," derives from the Latin *nubes* (cloud) and *colo* (dwell, inhabit) and is applied here in reference to the species' distribution in cloud forests present on mountains that rise above the surrounding lowlands of northwestern Costa Rica (Brown, 1956: 213, 478).

DISTRIBUTION: Known only from the Cordillera de Tilarán and Cordillera de Guanacaste of northwestern Costa Rica (fig. 4). In the Monteverde region of the Cordillera de Tilarán, it is found from 750 to 1840 m on the Caribbean slope and from 1350 to 1840 m on the Pacific slope. In the Cordillera de Guanacaste, the species has been collected at 1100–1500 m on Cerro Cacao and from 800 to 1200 m on Volcán Rincón de la Vieja–Volcán Santa María. See also Sympatry and Zones of Contact with *Heteromys desmarestianus*, below.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters (figs. 3, 5, 6, 7): p4 (lower permanent premolar) with 3 lophs; P4 (permanent upper premolar) with long, curved fold in anterior border of posterior loph; mesopterygoid fossa V-shaped, with long, thin hamular processes of pterygoids; optic foramen small, with exterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point; braincase not inflated; interorbit narrow; rostrum long and cylindrical; skull large (ONL 35.72–41.02 mm in adult specimens of age class 4; tables 1, 2), elongated and relatively narrow; body size average to large for genus; dorsal pelage soft to moderately spiny; dorsal coloration dark brown and only faintly grizzled with thin ochraceous hairs intermixed among spines; no lateral ochraceous band present on flanks; plantar surface of hind feet naked.

DESCRIPTION: Dorsal pelage (fig. 5) soft to moderately spiny and dark brown (sharply contrasting with soft, pure white pelage of venter), only faintly grizzled with thin ochraceous hairs intermixed among spines (grizzling generally less pronounced along midline, producing slight dorsal stripe); ears dark brown to dark gray and small to medium in size; tail strongly bicolored for most of its length (then unicolored dark distally), generally longer than head-and-body length (tables 1, 2); patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ventral and internal surfaces of forearms white; hind feet large (35 mm or greater in adults; tables 1, 2), with naked plantar surface; skull (figs. 3, 6, 7) moderately large for genus (tables 1, 2); anterior half of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum (in dorsal view); rostrum long and cylindrical (not tapered anteriorly or with dorsal flare anteriorly); nasals inflated anteriorly; interorbital constriction narrow; braincase narrow, not inflated; parietal and temporal crests weakly to moderately developed; interparietal moderately wide, often with slight anterior point; incisive foramina generally thin and slightly tapering anteriorly; no swelling at posteroventral border of infraorbital foramen[5]; mesopterygoid fossa V-shaped, with long, thin hamular processes of pterygoids; shallow parapterygoid fossa; postalar

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[5] Erroneously listed as "anterodorsal border of infraorbital foramen" in Anderson (2003b). In most species of *Liomys*, a distinct swelling is present at the posteroventral border of the infraorbital foramen (generally anterodorsal to the incisive foramina). Such a swelling is never present in species of *Heteromys*. Other, more salient and consistent differences between the two genera are listed in Anderson (2003b: 11).

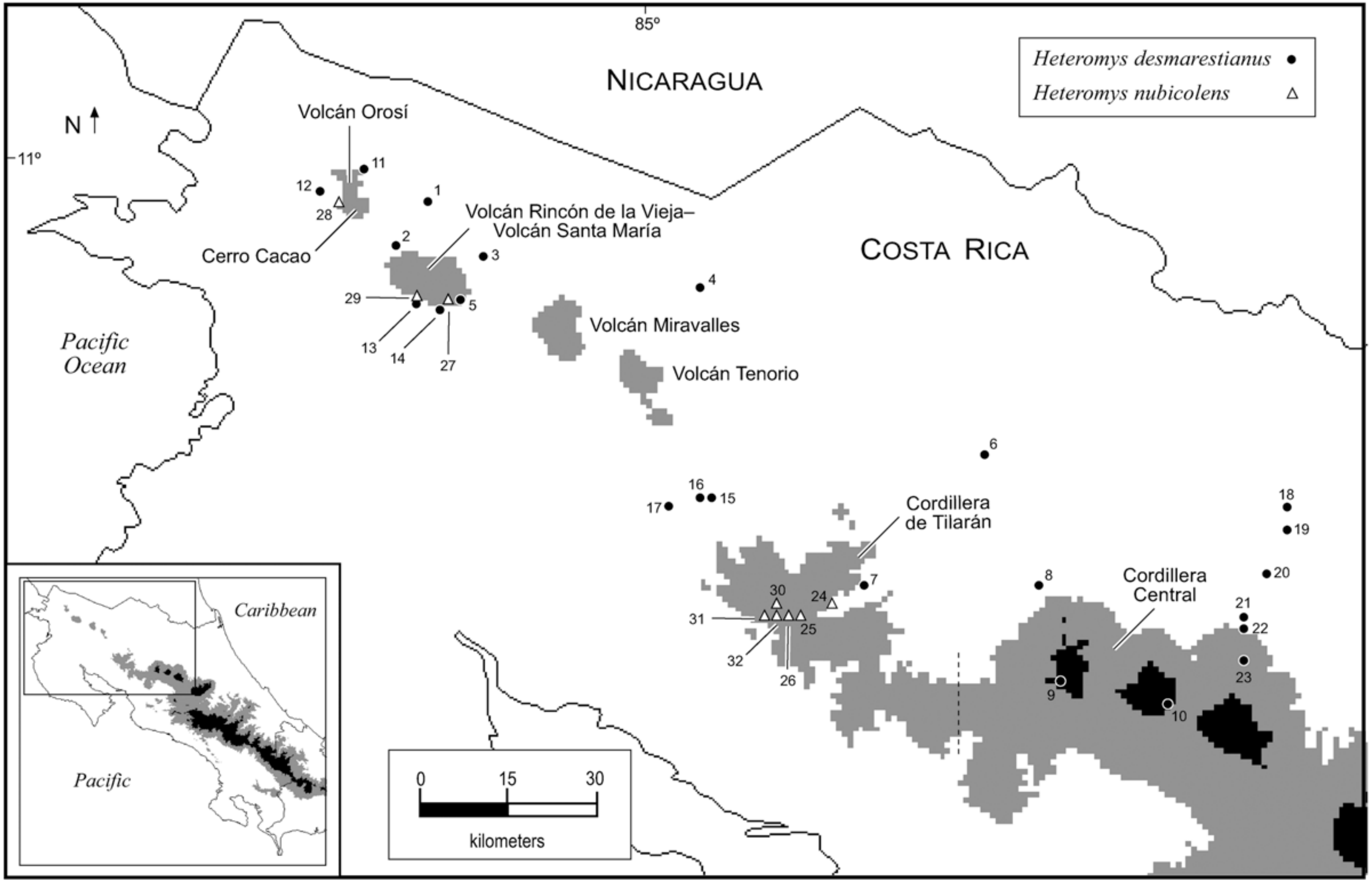

Fig. 4. Map showing collection localities for *Heteromys* in northwestern Costa Rica. Circles represent localities of *Heteromys desmarestianus*, and triangles denote localities of *H. nubicolens*. Localities are numbered to correspond to data given in the Gazetteer (appendix 1). Gray shading denotes regions higher than 1000 m in elevation, and areas shown in black lie above 2000 m.

fissure large and distinctly rounded anteriorly; optic foramen small, with exterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point; anterodorsal lobe of periotic capsule of mastoid well developed, causing distinct undulation in posterior margin of squamosal (see schematic drawing in Anderson, 1999: 619); jugular foramen (anterolateral to occipital condyle) medium in size; dental formula: (incisors 1/1, canines 0/0, premolars 1/1; molars 3/3) × 2 = total 20; molars moderately robust, with lophs of M2 subequal in width; lateral borders of lophs of molars smooth, not pointed; P4 with long, curved fold in anterior border of posterior loph, and with smoothly curved posterior border; p4 with 3 lophs; m3 not reduced, approximately same width as p4; angular process of mandible flat and blunt.

MEASUREMENTS OF THE HOLOTYPE (mm): total length 295, tail length 165, hind foot length 38, ear length 17, ONL 37.43, ZB 17.23, RL 17.45, NL 15.63, IOC 9.23, SB 16.12, MTR 5.38, IW 9.64, IL 5.26, PB 13.77, SD 11.42. Mass 68 g.

KARYOLOGY: Rogers (1989) reported the standard karyotype for two specimens now known as *Heteromys nubicolens* (from Provincia de Puntarenas: Monteverde, John Campbell's woods, MVZ 161224, 161225; appendix 1). This karyotype, the cytotype F of Rogers (1989), has a diploid number of 2n = 60 and a fundamental number of FN = 86.

COMPARISONS: Externally, the dark brown, moderately grizzled pelage of *Heteromys nubicolens* differentiates it from most currently recognized species of the genus (fig. 5). *Heteromys gaumeri*, *H. oasicus*, and most populations of *H. anomalus* have pale brown dorsal pelage that is strongly grizzled with thin ochraceous hairs intermixed among the spines (Anderson, 2003b). In addition, specimens of *H. gaumeri* possess a lateral ochraceous band that is absent in *H. nubicolens*. *Heteromys nubicolens* is much larger than the dwarf species *H. oasicus* (total length 227–250 mm for adults in age class 4; Anderson 2003b). *Heteromys gaumeri* is restricted geographically to Belize, Guatemala, and the Península de Yucatán in Mexico, and *H. anomalus* and *H. oasicus* inhabit only South America (Williams et al., 1993; Anderson, 2003b). Quite the reverse, *H. australis*, *H. nelsoni*, *H. oresterus*, and *H. teleus* show a dark slaty-gray, nearly uniform dorsal pelage, which separates them from the dark brown, moderately grizzled pelage of *H. nubicolens*. *Heteromys teleus* and *H. australis* are South American species, with the latter also showing a marginal distribution in extreme eastern Panama (Anderson, 1999; Anderson and Jarrín-V., 2002). Both *H. nelsoni* and *H. oresterus* display extremely soft dorsal pelage and are distributed in restricted highland regions of extreme southeastern Mexico and southwestern Guatemala (*H. nelsoni*) and the Cordillera de Talamanca in Costa Rica (*H. oresterus*; Rogers and Rogers, 1992; Williams et al., 1993; Reid, 1997). However, *H. nubicolens* is quite similar in external morphology to species of the *H. desmarestianus* complex, which ranges from southern Mexico (Estado de Veracruz) to extreme northwestern Colombia (Williams et al., 1993). Many populations of this complex possess a lateral ochraceous band that is absent in *H. nubicolens*, but comparisons are best made using cranial characters.

Cranial characters serve to separate *Heteromys nubicolens* from all other species of the genus (figs. 3, 6, 7). *Heteromys nubicolens* differs from *H. gaumeri* by the narrow postalar fissure and strongly concave anterior termination of the premaxillary of *H. gaumeri*. The formation of the premaxillary in *H. gaumeri* creates a distinct step in the lateral border of the rostrum in dorsal view, a character lacking in the new species. *Heteromys nubicolens* contrasts with the South American species *H. anomalus*, *H. australis*, *H. oasicus*, and *H. teleus* by the especially small optic foramen and the straight, only moderately long fold in the anterior border of the posterior loph of P4 of those species. *Heteromys nubicolens* is average in size for the genus (tables 1, 2), not nearly as large as the massive *H. nelsoni* (Williams et al., 1993).

Heteromys oresterus is similar to *H. nubicolens* in many respects but shows several clear differences. As mentioned above, *H. oresterus* has dark slaty-gray, nearly uniform dorsal pelage, in contrast to the dark brown, moderately grizzled pelage of *H. nubicolens*. Additionally, *H. oresterus* shows extremely

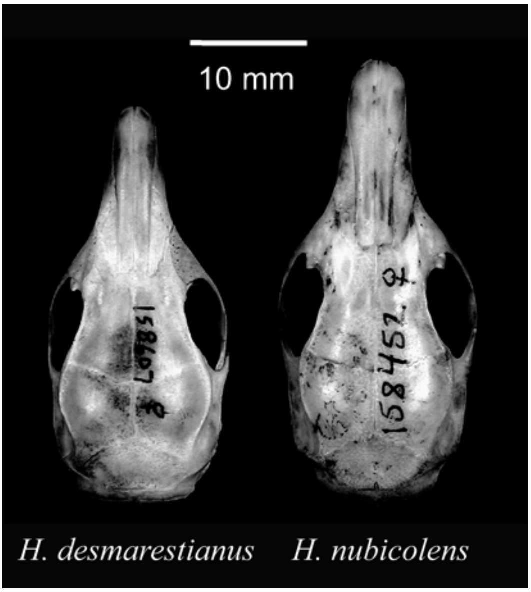

Fig. 6. Dorsal views of the crania of adult female specimens in age class 4 of two species of *Heteromys* from the slopes of Volcán Rincón de la Vieja–Volcán Santa María: *Heteromys desmarestianus*, 800 m (left, KU 158607; locality 13) and *H. nubicolens*, 1100 m (right, KU 158452; locality 27). See appendix 1 for full provenience.

soft dorsal pelage, whereas the dorsal pelage of *H. nubicolens* is soft-to-moderately spiny. Although spininess often varies clinally with elevation within a species of *Heteromys* (spinier in the lowlands and softer at higher elevations; Anderson, 1999: 619, 2003b: 23, 26; Anderson and Jarrín-V., 2002: 12), the difference in spininess between these two species is marked, despite the fact that they occur at broadly overlapping elevations. Cranially, *H. oresterus* differs by having an especially long, narrow rostrum (fig. 7) with a distinctive dorsal flare at the anterior termination of the rostrum (best observed in lateral view). Additionally, *H. oresterus* has deep parapterygoid fossae, in contrast to the shallow ones of *H. nubicolens*. In quantitative comparisons, *H. oresterus* averages larger than *H. nubicolens* in total length, head-and-body length, hind foot length, and occipitonasal length, but its average for the tail/head-and-body length ratio is smaller than that of *H. nubicolens* ($P < 0.041$ for significant comparisons, despite small sample size for *H. oresterus*). Other quantitative comparisons between these two species were nonsignificant ($P > 0.084$; test not possible for mass; see tables 1–3 for descriptive statistics). In addition to these external, cranial, and mensural differences, *H. oresterus* and *H. nubicolens* also differ in standard karyotype; whereas the diploid number for each species is $2n = 60$, the fundamental number for *H. oresterus* is $FN = 78$, in contrast to the $FN = 86$ of *H. nubicolens* (Rogers, 1989).

A member of the *Heteromys desmarestianus* complex comes into geographic contact with *H. nubicolens* in northwestern Costa Rica (see Sympatry and Zones of Contact with *Heteromys desmarestianus*, below) and merits close comparisons (figs. 6, 7). Currently, many species-level taxa are considered synonyms of *H. desmarestianus* (Williams et al., 1993; appendix 2), but none of them corresponds to the species here described as *H. nubicolens*. The two species present in northwestern Costa Rica are extremely similar externally, but differ in cranial size and proportions. Although both possess dark brown moderately grizzled dorsal pelage, that of *H. nubicolens* is generally less grizzled. In particular, very few ochraceous hairs are present along the midline of *H. nubicolens*, producing a gray dorsal stripe that is lacking in adjacent populations of *H. desmarestianus*. In addition, at Poco Sol (locality 7; appendix 1) near where the two species' distributions apparently come into contact in the Peñas Blancas Valley (see locality 24 of *H. nubicolens*), the ochraceous hairs of *H. desmarestianus* are especially pronounced around the neck, creating a "collar" not present in *H. nubicolens* (especially notable in the field; C.M. McCain, personal com-

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Fig. 5. External features of *Heteromys nubicolens* from Monteverde (KU 142791, paratype), an adult female in age class 5. Close-up views of the cheek pouches, left front foot, and left hind foot are also provided. Illustration made from life by Fiona A. Reid on 25 February 1987 and reproduced here with her permission. See appendix 1 for full provenience.


10 mm
age class 5
age class 4
age class 2
H. desmarestianus
H. nubicolens
H. oresterus

mun.). Otherwise, the two species are virtually identical in external coloration. Interestingly, *H. nubicolens* and *H. desmarestianus* exhibit vastly different behaviors when handled. *Heteromys desmarestianus* is quite vocal, uttering an array of audible sounds and actively struggling when held, whereas individuals of *H. nubicolens* make no audible vocalizations when handled and are quite passive (M. Klaus, personal commun.; C.M. McCain, personal commun.).

Quantitative comparisons document differences in size and shape between *Heteromys nubicolens* and *H. desmarestianus*. Although the two species overlap for mass and all external and cranial measurements, means were significantly different for each variable except ear length ($P < 0.002$ for significant comparisons; $P = 0.75$ for ear length; table 1). Generally, *H. nubicolens* is larger, but least interorbital constriction, interparietal length, and parietal breadth average greater for *H. desmarestianus* (see also figs. 6, 7). Accordingly, although overlap occurs, the species also differ in mean for the ratios of least interorbital constriction/occipitonasal length and parietal breadth/occipitonasal length ($P < 0.0001$). Indeed, the species barely overlap in a plot of least interorbital constriction versus occipitonasal length (fig. 8). In addition, *H. nubicolens* shows a larger tail/head-and-body length ratio ($P = 0.0006$).

Multivariate analyses also support the morphological distinctiveness of *Heteromys nubicolens* from *H. desmarestianus*. Only moderate overlap occurs between specimens of the two species in a plot of scores on the first two principal components of the PCA undertaken on specimens in age class 4 (fig. 9). The coefficients and loadings of PC1 are all of the same sign (table 4). Hence, we interpret that PC1 represents a size axis (with larger specimens having lower scores, because the signs of the coefficients are all negative). In contrast, PC2 represents a shape axis (because some coefficients are positive and others negative; table 4).

In sum, adults of *Heteromys nubicolens* show larger overall body size than *H. desmarestianus* and differ in cranial proportions (figs. 6, 7). Although most measurements are larger for *H. nubicolens*, specimens of *H. desmarestianus* have wider interorbits, longer interparietals, and wider braincases (see parietal breadth; tables 1, 2). In addition to these characters, direct visual comparisons of skulls indicate several further differences between the two species. The nasals flare laterally as they approach their anterior termination in *H. nubicolens*, whereas they are subparallel in *H. desmarestianus*. This character, combined with the overall greater development of the rostrum in *H. nubicolens*, yields a more massive rostrum that is both absolutely and relatively longer and less tapered anteriorly (in dorsal view) than that of *H. desmarestianus*. Because of its long rostrum, the interorbital constriction of *H. nubicolens* occupies a position proportionately more posterior than in *H. desmarestianus*. Additionally, associated with the wide interorbit and braincase of *H. desmarestianus*, the parietal and temporal crests tend to converge anteriorly in a V-shape in that species, in contrast to the generally hourglass-shaped crests of *H. nubicolens*. Overall, the parietal and temporal crests are more strongly developed in *H. desmarestianus*, forming a conspicuous shelf along the lateral borders of the interorbital constriction (whereas the corresponding crest is only weakly developed in *H. nubicolens*). Ventrally, the parapterygoid fossa is shallow in *H. nubicolens*, but deep in *H. desmarestianus*. Finally, the basisphenoid and basioccipital are wider at the level of the basisphenoid–basioccipital suture in *H. nubicolens* than in *H. desmarestianus*.

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Fig. 7. Comparisons of female specimens of *Heteromys desmarestianus* (left column), *H. nubicolens* (middle column), and *H. oresterus* (right column); dorsal views of the crania are provided for specimens in age class 5 (top row), age class 4 (middle row), and age class 2 (bottom row). Museum catalog numbers follow: age class 5, KU 158510, KU 142791, and MVZ 164860 (note, zygomatic arches are missing due to breakage); age class 4, KU 158505, KU 159025 (holotype of *H. nubicolens*), and MVZ 164861; age class 2, MNCR 793, MNCR 797, and MVZ 164862. See appendices 1 and 2 for full provenience.

TABLE 1

Descriptive Statistics and Results of *t*-Tests Comparing Adults in Age Class 4 of *Heteromys desmarestianus* and *H. nubicolens* in Northwestern Costa Rica for External Measurements, Mass, Cranial Measurements, and Three Derived Ratios[a]

	H. desmarestianus	*H. nubicolens*
Total length****	292.2 ± 3.9, 46 (238–353)	322.2 ± 2.7, 41 (291–358)
Head-and-body length**	138.7 ± 1.9, 52 (96–169)	146.4 ± 1.5, 52 (104–183)
Tail length****	152.8 ± 2.6, 46 (128–210)	174.8 ± 1.7, 41 (150–197)
Tail/head-and-body ratio, × 100 (%; ***)	110.0 ± 1.8, 46 (90.8–146.9)	119.3 ± 1.9, 41 (95.6–179.8)
Hind foot length****	35.8 ± 0.3, 52 (32–40)	38.7 ± 0.2, 51 (35–42)
Ear length (n.s.)	17.9 ± 0.2, 51 (13–20)	17.8 ± 0.2, 51 (15–21)
Mass (grams)**	75.4 ± 2.7, 42 (37–110)	86.6 ± 2.4, 50 (60–136)
Occipitonasal length****	36.506 ± 0.109, 176 (32.71–40.09)	38.630 ± 0.177, 51 (35.72–41.02)
Zygomatic breadth****	16.519 ± 0.054, 134 (15.20–18.52)	17.533 ± 0.085, 42 (16.40–18.51)
Rostral length****	16.558 ± 0.062, 176 (14.51–18.67)	17.950 ± 0.110, 50 (15.82–19.36)
Nasal length****	15.283 ± 0.065, 175 (13.05–17.25)	16.079 ± 0.112, 51 (13.89–17.78)
Least interorbital constriction****	9.789 ± 0.036, 176 (8.39–11.11)	9.250 ± 0.067, 51 (8.20–10.40)
Squamosal breadth****	15.471 ± 0.032, 176 (14.40–16.59)	15.932 ± 0.059, 51 (15.19–17.74)
Maxillary toothrow length****	5.252 ± 0.017, 176 (4.63–5.99)	5.461 ± 0.035, 51 (4.97–5.92)
Interparietal width****	9.289 ± 0.042, 176 (8.02–10.75)	9.715 ± 0.066, 51 (8.24–10.84)
Interparietal length****	5.288 ± 0.033, 176 (4.23–6.49)	4.912 ± 0.071, 51 (3.82–6.11)
Parietal breadth****	14.286 ± 0.033, 176 (13.11–15.50)	13.795 ± 0.045, 51 (12.85–14.60)
Skull depth****	11.202 ± 0.023, 176 (10.43–11.99)	11.640 ± 0.032, 51 (11.00–12.09)
Least interorbital constriction/ occipitonasal length ratio, × 100 (%; ****)	26.824 ± 0.076, 176 (23.93–28.79)	23.944 ± 0.133, 51 (22.20–26.46)
Parietal breadth/ occipitonasal length ratio, × 100 (%; ****)	39.164 ± 0.093, 176 (35.38–41.80)	35.742 ± 0.175, 51 (32.63–38.94)

[a] Mean ± standard error, sample size, and observed range (minimum–maximum) are given for each species. Measurements with significant differences in two-tailed *t*-tests comparing means of the species are indicated (* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; n.s. = $P > 0.05$). Note that whereas averages of most measurements are larger for *H. nubicolens*, averages for least interorbital constriction, interparietal length, and parietal breadth are larger in *H. desmarestianus*. Units are millimeters unless otherwise noted.

GEOGRAPHIC VARIATION: Moderate geographic variation exists between samples of *Heteromys nubicolens* from the Cordillera de Tilarán versus those of the Cordillera de Guanacaste (table 2). Means for a few measurements were significantly different in univariate comparisons of specimens from Monteverde (localities 30–32; Cordillera de

TABLE 2

Descriptive Statistics for Adults in Age Class 4 of *Heteromys desmarestianus* from La Selva and *H. nubicolens* from Monteverde and Cerro Cacao in Northwestern Costa Rica[a]

	La Selva	Monteverde	Cerro Cacao
Total length	265, 1 (265)	318.9 ± 4.1, 17 (291–347)	329.3 ± 3.5, 15 (300–351)
Head-and-body length	131, 1 (131)	143.2 ± 2.2, 27 (104–163)	150.3 ± 1.5, 15 (140–158)
Tail length	134, 1 (134)	175.1 ± 2.6, 17 (153–192)	179.1 ± 2.7, 15 (155–197)
Tail/head-and-body ratio, × 100 (%)	102.3, 1 (102.3)	122.8 ± 3.9, 17 (105.1–179.8)	119.2 ± 1.8, 15 (106.9–131.4)
Hind foot length	35, 1 (35)	38.9 ± 0.3, 26 (35–41)	38.7 ± 0.4, 15 (36–42)
Ear length	17, 1 (17)	17.8 ± 0.2, 27 (16–21)	18.3 ± 0.3, 14 (17–20)
Mass (grams)	62, 1 (62)	79.4 ± 2.2, 26 (61–109)	104.9 ± 3.5, 14 (90–136)
Occipitonasal length	36.512 ± 0.123, 121 (32.71–39.74)	38.346 ± 0.210, 28 (36.48–40.49)	39.183 ± 0.376, 13 (35.72–41.02)
Zygomatic breadth	16.359 ± 0.059, 85 (15.20–17.83)	17.413 ± 0.110, 24 (16.40–18.31)	17.831 ± 0.227, 8 (16.52–18.51)
Rostral length	16.590 ± 0.069, 121 (14.51–18.45)	17.786 ± 0.125, 27 (16.61–19.29)	18.270 ± 0.234, 13 (15.82–19.11)
Nasal length	15.365 ± 0.070, 121 (13.21–17.25)	15.999 ± 0.154, 28 (13.89–17.78)	16.265 ± 0.213, 13 (14.25–17.41)
Least interorbital constriction	9.919 ± 0.038, 121 (8.75–11.11)	9.222 ± 0.088, 28 (8.37–10.19)	9.419 ± 0.093, 13 (8.78–10.04)
Squamosal breadth	15.449 ± 0.036, 121 (14.40–16.35)	15.971 ± 0.061, 28 (15.43–16.61)	15.746 ± 0.075, 13 (15.19–16.26)
Maxillary toothrow length	5.237 ± 0.020, 121 (4.63–5.78)	5.516 ± 0.041, 28 (5.02–5.85)	5.268 ± 0.050, 13 (4.97–5.51)
Interparietal width	9.270 ± 0.044, 121 (8.03–10.23)	9.906 ± 0.079, 28 (9.14–10.84)	9.425 ± 0.102, 13 (8.88–10.00)
Interparietal length	5.274 ± 0.037, 121 (4.29–6.40)	4.858 ± 0.094, 28 (3.82–5.98)	4.999 ± 0.169, 13 (3.94–6.11)
Parietal breadth	14.387 ± 0.038, 121 (13.26–15.50)	13.712 ± 0.064, 28 (12.85–14.45)	13.878 ± 0.092, 13 (13.21–14.60)
Skull depth	11.212 ± 0.025, 121 (10.43–11.99)	11.636 ± 0.044, 28 (11.00–12.09)	11.635 ± 0.060, 13 (11.07–11.88)
Least interorbital constriction/ occipitonasal length ratio, × 100 (%)	27.171 ± 0.069, 121 (25.20–28.79)	24.045 ± 0.171, 28 (22.41–26.06)	24.048 ± 0.217, 13 (22.76–25.48)
Parietal breadth/ occipitonasal length ratio, × 100 (%)	39.429 ± 0.100, 121 (36.68–41.56)	35.787 ± 0.250, 28 (32.63–38.94)	35.444 ± 0.300, 13 (33.69–37.34)

[a] Mean ± standard error, sample size, and observed range (minimum–maximum) are given for external measurements, mass, cranial measurements, and three derived ratios. Units are millimeters unless otherwise noted. La Selva (localities 18, 19), Monteverde (localities 30–32; all on the Pacific slope or crest of the Cordillera de Tilarán), and Cerro Cacao (locality 28) constituted the geographic samples (see appendix 1).

Tilarán) with those from Cerro Cacao (locality 28; Cordillera de Guanacaste). Externally, only head-and-body length ($P = 0.01$; longer at Cerro Cacao) and mass ($P < 0.0001$; larger at Cerro Cacao) differed. In two cranial dimensions reflecting aspects of the width of the neurocranium, the Monteverde sample averaged larger (squamosal breadth, $P = 0.027$; interparietal width, $P = 0.0009$). Finally, the samples differed in mean for maxillary toothrow length ($P = 0.0006$; longer at Monteverde).

TABLE 3

Descriptive Statistics for Adults in Age Class 4 of *Heteromys oresterus* in Central Costa Rica for External Measurements, Mass, Cranial Measurements, and Three Derived Ratios[a]

	All specimens	El Copey de Dota (type locality)
Total length	339.9 ± 6.8, 7 (311–357)	343.5 ± 6.7, 6 (311–357)
Head-and-body length	164.8 ± 5.3, 8 (143–183)	168.8 ± 6.1, 6 (143–183)
Tail length	174.4 ± 1.9, 8 (168–185)	175.0 ± 2.0, 7 (168–185)
Tail/head-and-body ratio, × 100 (%)	105.7 ± 3.8, 7 (95.1–117.5)	104.2 ± 4.1, 6 (95.1–117.5)
Hind foot length	39.9 ± 0.2, 9 (39–41)	39.9 ± 0.3, 7 (39–41)
Ear length	17.0 ± 0.6, 9 (14–20)	16.7 ± 0.7, 7 (14–20)
Mass (grams)	74.0, 1 (74)	— (—)
Occipitonasal length	39.554 ± 0.364, 9 (38.22–40.91)	39.901 ± 0.368, 7 (38.26–40.91)
Zygomatic breadth	17.597 ± 0.162, 4 (17.37–18.07)	17.735 ± 0.335, 2 (17.40–18.07)
Rostral length	18.419 ± 0.224, 9 (17.34–19.40)	18.566 ± 0.252, 7 (17.34–19.40)
Nasal length	16.222 ± 0.181, 9 (15.65–16.97)	16.381 ± 0.194, 7 (15.65–16.97)
Least interorbital constriction	9.308 ± 0.159, 9 (8.72–10.07)	9.410 ± 0.184, 7 (8.72–10.07)
Squamosal breadth	16.106 ± 0.087, 9 (15.69–16.59)	16.113 ± 0.112, 7 (15.69–16.59)
Maxillary toothrow length	5.457 ± 0.070, 9 (5.17–5.76)	5.454 ± 0.065, 7 (5.20–5.65)
Interparietal width	9.893 ± 0.194, 9 (8.84–10.64)	10.053 ± 0.184, 7 (9.17–10.64)
Interparietal length	5.159 ± 0.150, 9 (4.54–6.03)	5.319 ± 0.138, 7 (4.96–6.03)
Parietal breadth	13.887 ± 0.079, 9 (13.47–14.17)	13.847 ± 0.097, 7 (13.47–14.17)
Skull depth	11.736 ± 0.092, 9 (11.41–12.16)	11.763 ± 0.107, 7 (11.47–12.16)
Least interorbital constriction/ occipitonasal length ratio, × 100 (%)	23.522 ± 0.240, 9 22.436–24.615	23.573 ± 0.298, 7 22.436–24.615
Parietal breadth/ occipitonasal length ratio, × 100 (%)	35.134 ± 0.407, 9 33.120–36.609	34.721 ± 0.395, 7 33.120–35.883

[a] Mean ± standard error, sample size, and observed range (minimum–maximum) are given for all available specimens and for specimens from the type locality (El Copey de Dota; see appendix 2). Units are millimeters unless otherwise noted.

Sympatry and Zones of Contact with *Heteromys desmarestianus*: Presently available specimens document three regions where the distribution of *Heteromys nubicolens* comes into geographic contact with that of *H. desmarestianus*, including one site of sympatry (fig. 4). The two species show parapatric distributions in the foothills of the Peñas Blancas Valley (on the Caribbean slope of the Cordillera de Tilarán in the Monteverde region) and at intermediate elevations on the slopes of both Cerro Cacao and Volcán Rincón de la Vieja–Volcán Santa María (in the Cordillera de Guanacaste; see

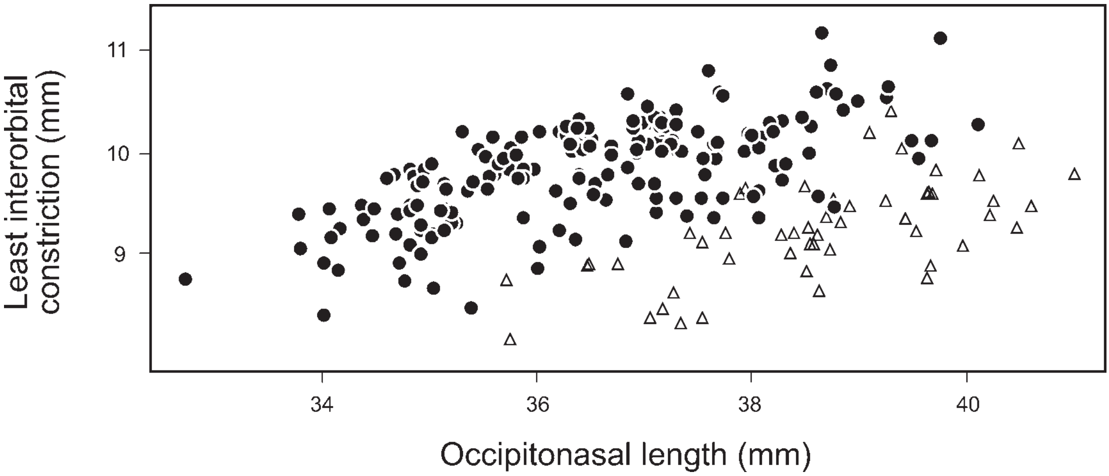

Fig. 8. Plot of least interorbital constriction versus occipitonasal length for adult specimens of *Heteromys* in age class 4 from northwestern Costa Rica. Circles represent individuals of *H. desmarestianus*, and triangles denote those of *H. nubicolens.*

also fig. 6). Similar parapatric distributions have been observed for other pairs of species in the subfamily (Genoways, 1973; Rogers and Engstrom, 1992; Anderson, 1999; Anderson et al., 2002b; Anderson and Jarrín-V., 2002; Anderson and Martínez-Meyer, 2004).

In the Peñas Blancas Valley on the Caribbean slope of the Cordillera de Tilarán in the Monteverde region, the species' distributions probably meet at ca. 750–1000 m (fig. 4). Along the main course of the Río Peñas Blancas, a recent standardized survey captured *Heteromys nubicolens* from the continental divide down to 750 m in elevation (localities 24–26, 30, 32; appendix 1; McCain, 2004, in press). In contrast, the same survey only encountered *H. desmarestianus* from 750 to 1050 m in elevation; these sites near the Poco Sol Field Station correspond to an area farther from the main valley (voucher specimens were collected at 750 m, locality 7, whereas captures of this species at 1000–1050 m were released; McCain, 2004; C.M. McCain, personal commun.).

On the slopes of Cerro Cacao in the Cordillera de Guanacaste, the species turn over at ca. 900–1100 m (fig. 4). At Cerro Cacao (locality 28; appendix 1), the new species has been collected from 1100 to 1500 m. *Heteromys desmarestianus* is known from Maritza, Sendero Cacao at 600–900 m (locality 12) on the western slopes of Volcán Orosí and Cerro Cacao (which share a common base, with their peaks being connected by a broad connection at ca. 1000 m). This *sendero* (trail) runs from the Maritza field station south to the Cerro Cacao field station (Estación Mengo), following a gradual ascent to ca. 900 m before rising steeply to the Cerro Cacao field station. Elsewhere in the general vicinity of Cerro Cacao, *H. desmarestianus* also is known from 600 to 900 m at Pitilla, Sendero Carica and Pitilla, Sendero Orosilito (locality 11). These trails rise from the Pitilla field station, which lies on the northeastern slope of Volcán Orosí.

On the slopes of Volcán Rincón de la Vieja–Volcán Santa María, the species' distributions turn over at ca. 800–1100 m, and one site of sympatry is known (figs. 4, 6). Here, collections of *Heteromys* exist from two areas, the southeastern and southwestern versants of the mountain. On a southeastern ridge, *H. nubicolens* has been collected at 1100 m (locality 27; appendix 1). Just below that site, *H. desmarestianus* is known from the Quebrada Provisión, 900–1000 m (locality 5) and from the Hacienda Santa María (locality 14). Goodwin (1946) gave the elevation of Hacienda Santa María as 3200 ft (= 975 m; Harris [1943] reported these specimens but did not give an elevation). Hence, in this area, *H. desmarestianus* appears to replace *H. nubicolens* at 1000–1100 m.

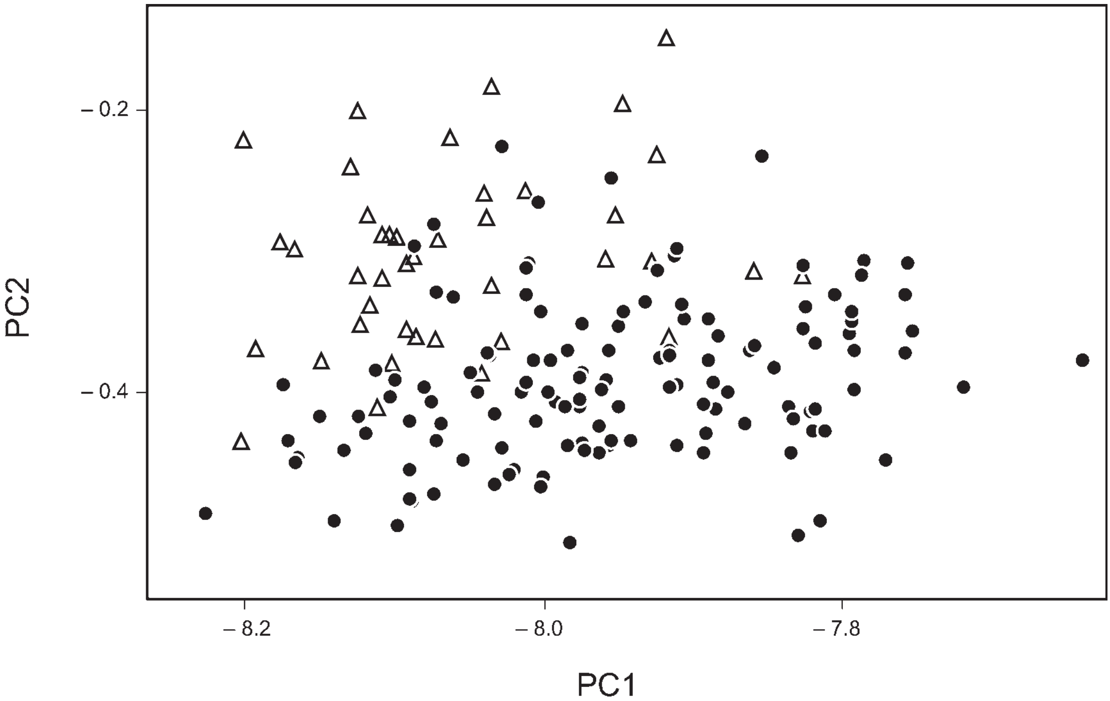

Fig. 9. Plot of specimen scores on the first two axes of a principal components analysis of cranial measurements of *Heteromys desmarestianus* (circles) and *H. nubicolens* (triangles) from northwestern Costa Rica. The analysis was performed on the covariance matrix of $\log_e$-transformed cranial measurements of adult specimens in age class 4. Axes are scaled relative to their eigenvalues (proportion of the variation among specimens explained).

Both species also are known from the southwestern slopes of Volcán Rincón de la Vieja–Volcán Santa María, including a site of sympatry at 800 m (note that locality 13 for *Heteromys desmarestianus* = locality 29 of *H. nubicolens*; figs. 4, 6; appendix 1). In this area, *H. nubicolens* has been collected at both Pailas, Sendero Cráter, 1200 m and Pailas, Sendero Pailas, near Río Colorado, 800 m (locality 29). These two trails emanate from the Pailas field station. *Heteromys desmarestianus* is known from Pailas, Sendero Pailas, 800 m (locality 13). In addition, two specimens that we tentatively ascribe to *H. desmarestianus* were collected from Pailas, Sendero Pailas, near Río Colorado, 800 m (locality 13). The skulls of these two individuals (KU 158614, 158615; adult females in age class 5) are smaller than those of *H. nubicolens* in the equivalent age class. Furthermore, they display most cranial characters typical of *H. desmarestianus*. However, the parietal and temporal crests are hourglass-shaped, and the rostrum is massive and not tapered anteriorly. We provisionally identify these specimens as *H. desmarestianus*, but raise the possibility that they may represent rare hybrids, present along a very narrow contact zone between the two species. Genetic studies are necessary to examine this possibility further.

NATURAL HISTORY: Whereas copious ecological information is available for *Heteromys desmarestianus* at La Selva (localities 18, 19; appendix 1) in Costa Rica (Fleming, 1974a, 1974b, 1977, 1983; Fleming and Brown, 1975; Vandermeer, 1979; Vandermeer et al., 1979; Timm, 1994) and for a few populations in other parts of the range of this species complex (e.g., Fleming, 1970; Quintero and Sánchez-Cordero, 1989; Sánchez-Cordero, 1993; Sánchez-Cordero and Fleming, 1993; Brewer and Rejmánek, 1999; Brewer, 2001), relatively little has been published regarding

TABLE 4
Results of Principal Components Analysis for Adult Specimens in Age Class 4 of *Heteromys desmarestianus* and *H. nubicolens* from Northwestern Costa Rica[a]

	Unit eigenvector			Loadings		
	PC1	PC2	PC3	PC1	PC2	PC3
ln-Occipitonasal length	−0.364	0.096	0.025	−0.941	0.201	0.027
ln-Zygomatic breadth	−0.301	0.135	−0.093	−0.794	0.289	−0.122
ln-Rostral length	−0.466	0.175	0.066	−0.906	0.277	0.057
ln-Nasal length	−0.469	0.095	0.187	−0.902	0.146	0.171
ln-Least interorbital constriction	−0.215	−0.209	0.652	−0.440	−0.339	0.654
ln-Squamosal breadth	−0.187	0.047	−0.046	−0.755	0.151	−0.095
ln-Maxillary toothrow length	−0.268	0.112	−0.108	−0.669	0.229	−0.138
ln-Interparietal width	−0.303	−0.007	−0.638	−0.564	−0.009	−0.583
ln-Interparietal length	−0.215	−0.919	−0.179	−0.288	−0.934	−0.118
ln-Parietal breadth	−0.097	−0.144	0.270	−0.343	−0.401	0.464
ln-Skull depth	−0.198	0.090	0.015	−0.772	0.283	0.027
Eigenvalue (× 100)	1.393	0.885	0.339			
% variation explained	42.9	27.2	10.5			

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

the species now known as *H. nubicolens*. Most of what is known derives from Monteverde and adjacent localities in the Cordillera de Tilarán. *Heteromys nubicolens* represents a common forest-floor species in the small mammal community at Monteverde (Ashe and Timm, 1987a; Timm and LaVal, 2000a). At Monteverde, adult *H. nubicolens* have a home range of ca. 0.15 ha and do not shift their home ranges appreciably even over several months; immatures have a smaller home range of ca. 0.10 ha (Anderson, 1982: 166). Breeding can occur during any month (Anderson, 1982). This species was captured at all elevations in a transect from 1840 m in the Monteverde region down the Peñas Blancas Valley to 750 m on the Caribbean slope of the Cordillera de Tilarán (McCain, 2004, in press).

Heteromys nubicolens appears to have a moderate tolerance for human-altered habitats. In many years of trapping at Monteverde by R.M.T., this species was often captured in primary forests above ca. 1500–1550 m, as well as in secondary forests 20–35 years old at ca. 1350–1550 m. However, despite extensive trapping in highly disturbed habitats, R.M.T. never captured *H. nubicolens* in pastures, farmed areas, or other highly disturbed areas. Some of the secondary forests at Monteverde represent former pastures that were planted with native tree species through projects aimed at restoring wildlife habitat or conserving soil and water. Other pastures were simply abandoned and allowed to regenerate on their own. Although Timm (1994: 232) reported "tremendous population fluctuations of spiny pocket mice at Monteverde" (see also Anderson, 1982), the species is generally captured in higher numbers in secondary forests than in primary ones (R.M.T., personal obs.).

Several decades of theriological research in the Monteverde area allow for characterization of the communities of small, nonvolant mammals in which *Heteromys nubicolens* occurs (Timm and LaVal, 2000a, 2000b; Woodman, 2000; Durden and Timm, 2001; Timm and Vriesendorp, 2003). In cloud forest, lower montane wet forest, and lower montane rainforest at Monteverde (ca. 1500–1850 m; Haber, 2000; Nadkarni and Wheelwright, 2000a) in the general vicinity of where the holotype of *H. nubicolens* was obtained, the following small, nonvolant mammals occur: the marsupials *Caluromys derbianus*, *Didelphis marsupialis*, and *Marmosa mexicana*; the shrews *Cryptotis nigrescens* and *C. merriami*;

the squirrels *Microsciurus alfari* and *Sciurus granatensis*; the pocket gopher *Orthogeomys cherriei*; and the sigmodontine rodents *Nyctomys sumichrasti*, *Oligoryzomys vegetus*, *Oryzomys devius* (= *O. albigularis*), *Peromyscus nudipes*, *Reithrodontomys creper*, *R. gracilis*, *Reithrodontomys* sp., *Rheomys raptor*, *Scotinomys teguina*, and *Tylomys watsoni*. Additional species of mammals that occur sympatrically with *H. nubicolens* in other (generally lower) parts of the Monteverde/Peñas Blancas region include: the marsupials *Micoureus alstoni* and *Philander opossum*; the squirrel *Sciurus variegatoides*; and the sigmodontine rodents *Melanomys caliginosus*, *Oligoryzomys fulvescens*, *Oryzomys alfari*, and *O. bolivaris*. In R.M.T.'s trapping at Monteverde, *P. nudipes* was usually the most common small rodent in habitats where *H. nubicolens* was found; *Oryzomys devius* and *Scotinomys teguina* were typically collected along with this species of *Heteromys* as well (see also McCain, 2004).

In contrast to the information available for the Cordillera de Tilarán, little has been published on the mammals of the Cordillera de Guanacaste and surrounding lowlands; hence, even basic natural history information is lacking for *Heteromys nubicolens* there. Studies of communities of small nonvolant mammals have been conducted recently by Marion Klaus (Sheridan College, Sheridan, WY) at various localities in the Área de Conservación Guanacaste (including Cerro Cacao and Volcán Rincón de la Vieja–Volcán Santa María). Similarly, Neal Woodman (Patuxent Wildlife Research Center, United States Geological Survey) conducted a series of mammalian inventories in the region in 1987–1988. Voucher specimens from those projects were included in the present taxonomic study; future work by Klaus and Woodman may provide ecological and natural history information on *Heteromys nubicolens* in this region.

ECTOPARASITES AND OTHER ASSOCIATED INVERTEBRATES: Two species of ectoparasites have been collected on *Heteromys nubicolens*. Both are ticks (Acarina: Ixodidae): *Ixodes venezuelensis* (from KU 158611) and *Dermacentor* sp. (from KU 158610 and KU 159026). Notably, two species of amblyopinine beetles (Coleoptera: Staphylinidae) that are commensal with other small mammals (*Oryzomys devius*, *Peromyscus nudipes*, and *Reithrodontomys creper*, and rarely on *Tylomys watsoni*) at Monteverde have not been found on *H. nubicolens* (Ashe and Timm, 1987a, 1987b, 1995; Timm and Ashe, 1988). Similarly, a tineid moth, *Amydria selvae*, is phoretic (a nonparasitic association where one organism attaches to the other for dispersal) on *H. desmarestianus* at La Selva (Davis et al., 1986) but has not been found on *Heteromys nubicolens* at Monteverde (R.M.T., personal obs.; Timm et al., 1989: 116). Finally, whereas pseudoscorpions of the genus *Epichernes* have been reported as phoretic on *H. gaumeri* and *Liomys salvini* (the latter in northwestern Costa Rica; Muchmore, 1992), none has been found on *H. nubicolens*.

CONSERVATION STATUS: Although we do not consider that *Heteromys nubicolens* currently needs additional special protection, future studies of its distribution and population sizes will allow for evaluation based on IUCN (2001) criteria.[6] All data available from field collectors indicate that *H. nubicolens* inhabits only closed-canopy forests (similar to *H. australis* and *H. teleus*; Anderson and Jarrín-V., 2002; Anderson and Martínez-Meyer, 2004), including both primary forests and secondary stands more than 20 years in age (see Natural History). Although middle- and high-elevation forests have been less affected by deforestation than lowland forests in Costa Rica, high average annual rates of forest conversion continue in the country (Sader and Joyce, 1988; Sánchez-Azofeifa et al., 2001). Fortunately, many areas in the range of *H. nubicolens* are protected by extensive private and governmental reserves. For purposes related to conservation, Costa Rica is divided administratively into a series of official conservation areas that cut across provincial borders (Janzen, 2000; Savage, 2002: 53; Mata and Echeverría, 2004). Within each conservation area, some regions correspond to national parks or other govern-

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[6] No species of heteromyine currently is included on Costa Rica's official lists of species with reduced populations or in danger of extinction (MINAE, 1999), although *Heteromys oresterus* is considered "near threatened" by the IUCN/UICN (Rodríguez-Herrera et al., 2002).

mentally protected areas, but other land remains in private hands (including private conservation reserves). Known localities of *H. nubicolens* fall in a complex of private reserves in the Monteverde region (in the Área de Conservación Arenal; Burlingame, 2000), as well as in the Parque Nacional Guanacaste and Parque Nacional Rincón de la Vieja (in the Área de Conservación Guanacaste; Janzen, 2000; Savage, 2002; Mata and Echeverría, 2004). In addition, yet-undiscovered populations of the species likely exist (see Biogeography, below) in the Parque Nacional Volcán Arenal, Parque Nacional Volcán Tenorio, and other governmentally protected areas in the Área de Conservación Arenal.

TAXONOMIC NOTES ON OTHER *HETEROMYS* IN COSTA RICA

HETEROMYS ORESTERUS: Our examinations indicate that *Heteromys oresterus* is known definitively from only three localities in the western portion of the Cordillera de Talamanca in central Costa Rica (fig. 10; appendix 2). In the original description, Harris (1932) named *H. oresterus* from El Copey de Dota, 6000 ft [1829 m] in the Provincia de San José [9°39′N, 83°55′W, McPherson, 1985]. In addition to the holotype, he made reference to eight other adult topotypes. The full series collected by Austin Smith in 1931 includes those nine adults plus one juvenal specimen (UMMZ 64026–64034, 66478) collected at elevations ranging from 6000 to 6500 ft [1829–1981 m]. In 1933, Smith obtained another specimen (UMMZ 67306) from a nearby locality on the Caribbean side of the continental divide in the Provincia de Cartago: El Muñeco, Río Navarro, 10 mi S of Cartago, 4300 ft [1311 m; 9°48′N, 83°53′W, McPherson, 1985]. A half century later, Duke S. Rogers and colleagues collected additional specimens in 1981 and 1982 from the Provincia de San José: 2.2 km E (by road) La Trinidad de Dota, 2600 m [9°40′N, 83°52′W, IGCR, 1963; MVZ 164860–164864, 165786; Mascarello and Rogers, 1988; Rogers, 1989, 1990; Rogers and Rogers, 1992]. We have examined the specimens from these three localities and concur that they all represent *H. oresterus* (appendix 2; see also figs. 7, 10).

However, other specimens from the Provincia de San José reported in the literature as *Heteromys oresterus* do not represent that species, but rather individuals of the *H. desmarestianus* species complex (fig. 10; appendix 2). These include a series collected by Alfred L. Gardner in 1967 from Fila la Máquina, ca. 7.5 km E El Canaan, 8700 ft [2652 m; 9°28′N, 83°34′W; McPherson, 1985; LSUMZ 13132–13138] considered to be *H. oresterus* by McPherson (1985) and Rogers and Rogers (1992). Furthermore, we tentatively reidentify a single specimen collected by R.M.T. in 1986 from 4 km S, 2 km E Ojo de Agua, 2535 m [9°35′N, 83°48′W; Ashe and Timm, 1987a; FMNH 128459] reported as *H. oresterus* by Rogers and Rogers (1992). These specimens lack the narrow (and dorsally flared) rostrum of *H. oresterus* and have a wider interorbital constriction than that species (fig. 7).

The subgeneric placement of *Heteromys oresterus* remains controversial and unclear. Only two subgenera (*Heteromys* and *Xylomys*) have been proposed for the genus *Heteromys*. *Xylomys* was initially described by Merriam (1902) for the distinctive species *H. nelsoni* (which is the largest in the genus and shows extremely soft dorsal pelage). Goldman (1911) listed several additional cranial characters that appeared to distinguish *Xylomys* based on the material available at the time. Subsequently, Hall and Kelson (1959) and Hall (1981) considered *H. oresterus* a member of the subgenus *Xylomys*. However, more recent work has shown that the only morphological character that unites *H. nelsoni* and *H. oresterus* is their possession of soft dorsal pelage (Rogers, 1986; Rogers and Rogers, 1992; see Homan and Genoways [1978] for morphology of heteromyid hair). Unfortunately, spininess often varies clinally with elevation within a species of *Heteromys*—spinier in the lowlands and softer at higher elevations (Anderson, 1999: 619, 2003b: 23, 26; Anderson and Jarrín-V., 2002: 12). Hence, we agree with Rogers (1986) and Rogers and Rogers (1992) in doubting the taxonomic utility of this character. No modern phylogenetic study of heteromyines has succeeded in determining the evolutionary relationships of the species of *Heteromys*, but morphological,

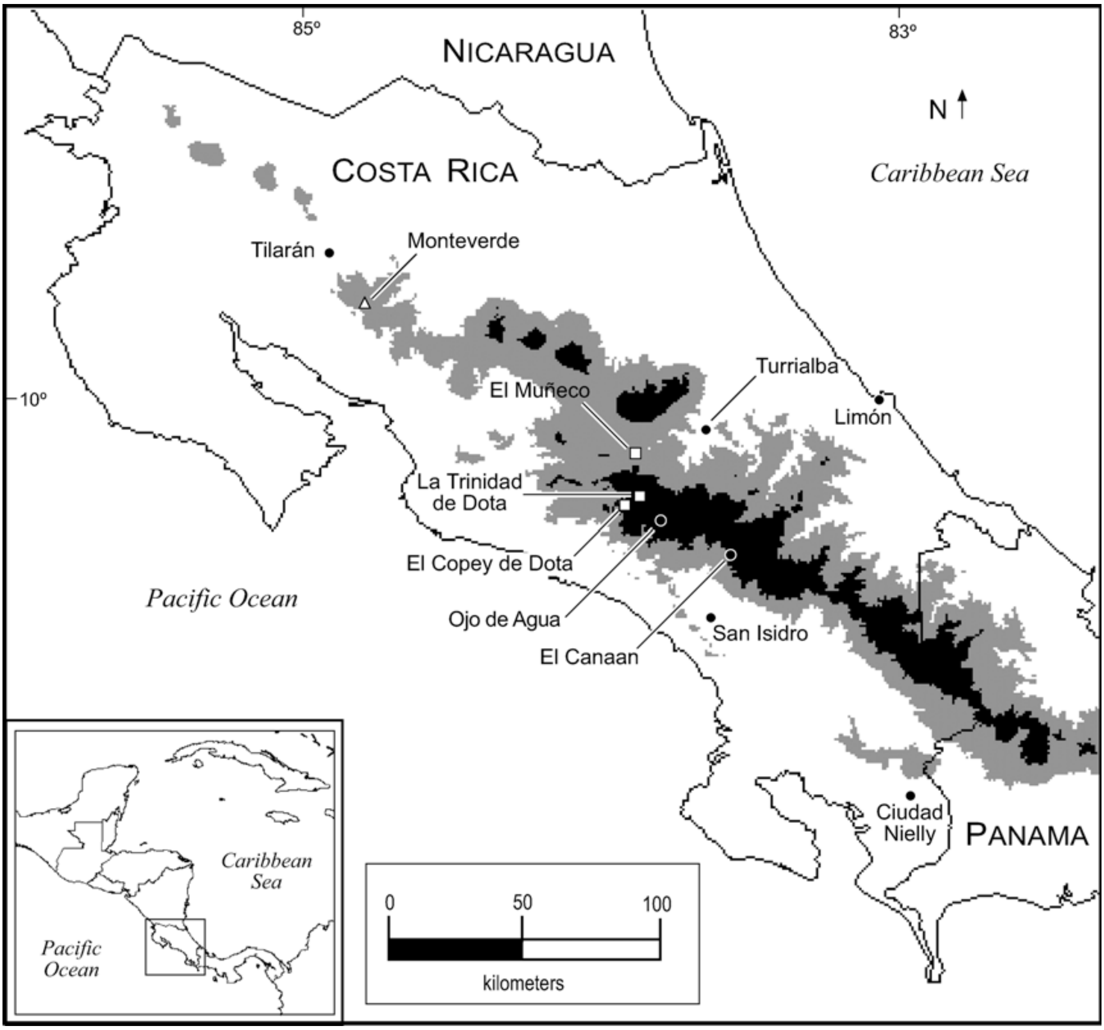

Fig. 10. Map showing selected collection localities for *Heteromys* in Costa Rica. Localities are plotted for voucher specimens from karyological and genetic studies (Mascarello and Rogers 1988; Rogers 1989, 1990). In addition, localities are plotted for confirmed specimens of *H. oresterus* and specimens previously reported as that species (McPherson, 1985; Rogers and Rogers, 1992). Circles represent localities of *H. desmarestianus*, the triangle denotes the locality of *H. nubicolens*, and squares indicate localities of *H. oresterus*. See appendices 1 and 2 for full provenience and specimen numbers. Gray shading denotes regions higher than 1000 m in elevation, and areas shown in black lie above 2000 m.

karyological, and genetic data suggest that *H. oresterus* is probably more closely related to members of the *H. desmarestianus* species complex than to *H. nelsoni* (Rogers, 1986: 186–191, 1989, 1990; Mascarello and Rogers, 1988). We conclude that recognition of defensible subgenera in *Heteromys* awaits the results of future phylogenetic analyses.

HETEROMYS DESMARESTIANUS SPECIES COMPLEX: Even after recognizing *Heteromys nubicolens* as a distinct species, *H. desmarestianus* remains a confusing complex of morphologically similar species that range from Mexico to Colombia and vary widely in karyology and protein allozymes. Except for *H. gaumeri* (2n = 56) and *H. nelsoni* (2n = 42), all *Heteromys* with known karyotypes have a diploid number of 2n = 60 (Engstrom et al., 1987; Rogers, 1989); however, the species with a diploid number of 2n = 60 vary widely in fundamental number (FN). At least nine karyotypic forms exist within the *H. desmarestianus* species complex (including *H. goldmani* and a sample of "*Heteromys* sp." from near Ciudad Nielly in southwestern Costa Rica; Mascarello and Rogers, 1988; Rogers, 1989; see also Genoways, 1973: 298; Burton et al., 1987; Engstrom et al., 1987). Four standard karyotypes are known from populations of *Heteromys* in Costa Rica (fig. 10; appendices 1, 2). The cytotype F of Rogers (1989) has a FN = 86 and was found for individuals from the Provincia de Puntarenas: Monteverde, John Campbell's woods (appendix 1) that represent the species now known as *H. nubicolens*. Cytotype F also was encountered in populations of the *H. desmarestianus* species complex from the Provincia de Guanacaste: 4.1–5 km NE (by road) Tilarán, 650 m (appendix 1) in northwestern Costa Rica and from the Provincia de Limón: 4.6 km W (by road) Limón, 25 m [9°59′N, 83°04′W, IGN, 1978] in southeastern Costa Rica (Rogers, 1989). The second variant, cytotype G of Rogers (1989), corresponds to samples of the *H. desmarestianus* species complex from the Provincia de Cartago: Río Reventazón, 5.6 km SE (by road) Turrialba, 450 m [9°53′N, 83°39′W, IGN, 1981] in southeastern Costa Rica, and it displays a FN = 80. Individuals of the *H. desmarestianus* species complex (*Heteromys* sp. of Rogers, 1989) from the Provincia de Puntarenas: 1.1 km SE (by road) Ciudad Nielly, 25 m [8°39′N, 82°57′W, IGN, 1980] in southwestern Costa Rica constitute the third moiety and show a FN = 90 (Rogers, 1989). By comparison, the karyotype of *H. oresterus* from the Provincia de San José: 2.2 km E (by road) La Trinidad de Dota, 2600 m (see above) in central Costa Rica has a FN = 78 (Rogers, 1989). In addition to these differences in fundamental number, individuals of the *H. desmarestianus* species complex from near Ciudad Nielly and from near Tilarán (see above) also differed strongly in karyological banding patterns (Mascarello and Rogers, 1988; Rogers, 1989). While karyological data alone cannot be used to elucidate species boundaries accurately (note similarity in standard karyotype between *H. nubicolens* and some populations of the *H. desmarestianus* species complex), these data reflect substantial cytogenetic discontinuities within the *H. desmarestianus* species complex.

Members of the *Heteromys desmarestianus* species complex also show extensive variation in protein allozymes (Rogers, 1990; based on many of the same individuals as the karyological studies cited above; fig. 10; appendices 1, 2). Two samples from southwestern Costa Rica referred to as *Heteromys* sp. showed a strong divergence in allozymes from other samples of the *H. desmarestianus* species complex: Provincia de Puntarenas: 1.1 km SE (by road) Ciudad Nielly, 25 m (see above; locality 16 of Rogers, 1990); Provincia de San José: 16.3 km SE (by road) San Isidro, 525 m [9°15′N, 83°38′W, IGN, 1970; locality 17 of Rogers, 1990]. These two samples were most similar to a sample of two individuals from eastern Panama in the Provincia del Darién: ca. 6 km NW Cana, E. slope Cerro Pirre, 1400 m [7°51′N, 77°44′W, Fairchild and Handley, 1966; locality 26 of Rogers, 1990; there considered *H. australis*]. These specimens from Panama represent a member of the *H. desmarestianus* species complex and were considered *H. d. crassirostris* by Anderson (1999). A single specimen from a slightly lower elevation (Provincia del Darién: ca. 6 km NW Cana, E. slope Cerro Pirre, 1200 m; locality 27 of Rogers, 1990; there considered *H. anomalus*) represents true *H. australis* (Anderson, 1999). Several species-level taxa described based on material from Costa Rica and Panama currently are considered synonyms of *H. desmarestianus* (Goodwin, 1946; Williams et al., 1993). Detailed specimen-based revisionary studies of alpha-level taxonomy are necessary to determine the true species limits in the *H. desmarestianus* species complex in central and eastern Costa Rica (and throughout Panama), clarify the synonymy of named forms, and determine the nomenclatural status of the species found near Ciudad Nielly and San Isidro.

DISCUSSION

BIOGEOGRAPHY

Complex climatic factors appear to influence the distribution of *Heteromys nubicolens*. A distinct rainy season runs from May to

December in northwestern Costa Rica, and rainfall is dramatically reduced during the rest of the year (Bergoeing, 1998). Furthermore, the spatial distribution of precipitation is far from homogenous throughout the region. Due to prevailing winds from the east, the Pacific slopes and lowlands lie in a strong rain shadow. Even at high elevations, rainfall is substantially higher on the Caribbean versant than on the Pacific one. In addition, horizontal precipitation in the form of mist provides considerable moisture all year at high elevations. On the wetter Caribbean slope in the Monteverde region (Peñas Blancas Valley), *H. nubicolens* ranges from 750 to 1840 m in elevation. On the corresponding rain-shadowed Pacific slope, however, it is known only from ca. 1350–1840 m (despite trapping by R.M.T. in forests at lower elevations there). In the Cordillera de Guanacaste, the species has been collected from 1100 to 1500 m in elevation on Cerro Cacao and from 800 to 1200 m on Volcán Rincón de la Vieja–Volcán Santa María (but likely ascends to the upper limits of forests on those peaks—due to recent volcanic activity, the summit of Volcán Rincón de la Vieja is not forested). Below the elevations where *H. nubicolens* exists, *H. desmarestianus* generally replaces it (see Sympatry and Zones of Contact with *Heteromys desmarestianus*). Similar parapatric distributions are also inferred for other pairs of species in the genus (Anderson, 1999; Anderson et al., 2002b; Anderson and Jarrín-V., 2002; Anderson and Martínez-Meyer, 2004).

Clearly, the lower distributional limits of *Heteromys nubicolens* do not correspond simply to elevation. In addition to elevation (which is highly correlated with temperature within a given region; Holdridge, 1967; Holdridge et al., 1971), the lower limit of *H. nubicolens* on various slopes is likely influenced by precipitation (both vertical and horizontal), as well as by the overall height of the range (climatic and vegetational bands are often lowered and compressed on smaller mountains; Massenerhebung effect; Richards, 1952: 346–374; Grubb and Whitmore, 1966; Grubb, 1977). Furthermore, it is not currently clear what role the seasonality of precipitation (versus total annual precipitation) drives these relationships, or what other biotic or abiotic factors may be involved. Another species of spiny pocket mouse, *Liomys salvini*, inhabits areas of high seasonality and overall low precipitation in deciduous habitats of the lowlands of western Costa Rica (Goodwin, 1946; Genoways, 1973; McPherson, 1985; Reid, 1997) to the west of the Cordillera de Tilarán and Cordillera de Guanacaste, where *H. nubicolens* and *H. desmarestianus* are found.[7] Unfortunately, the distributions of the three species of heteromyines present in northwestern Costa Rica have been altered by human modification of the landscape in many areas, hindering full reconstruction of their original ecogeographic distributions (cf. McPherson, 1985: 197).

Heteromys nubicolens is evidently endemic to the Cordillera de Tilarán and Cordillera de Guanacaste in northwestern Costa Rica (fig. 4). Significant theriological surveys have failed to capture the species in areas north of the Cordillera de Guanacaste or south of the Cordillera de Tilarán. Volcán Concepción and Volcán Madera, the two volcanoes immediately to the north of Volcán Orosí, form Isla de Ometepe in the Lago de Nicaragua in southern Nicaragua. This island was surveyed for small mammals recently, but no *Heteromys* was encountered there (Woodman et al., 2002). The presence of *H. nubicolens* in extensive highland areas north of the Nicaraguan lowlands seems even less likely. Similarly, *H. nubicolens* appears truly absent from the Cordillera Central of Costa Rica. Our present examination of museum specimens from northwestern Costa Rica yielded no records of *H. nubicolens* in the Cordillera Central, but confirmed many specimens of the *H. desmarestianus* species complex in montane habitats of that range (e.g., Timm et al., 1989). Interestingly, in the absence of *H. nubicolens* (in the Cordillera Central), *H. desmarestianus* inhabits higher elevations than it does in the Cordillera de Tilarán and Cordillera de Guanacaste, where *H. nubicolens* is present. This pattern hints of possible asymmetrical

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[7] McPherson (1985) reported an anomalous record of *Heteromys desmarestianus* from the arid western lowlands of the Provincia de Guanacaste: Río Bebedero, 2 km S Bebedero, 20 m. We examined this specimen (KU 88246) and confirm it as *Liomys salvini* (as originally reported by Genoways, 1973: 240, who gave the elevation as 5 m, in agreement with the KU catalog).

competitive relationships between the two species (see Anderson et al., 2002b for tests of such phenomena in *H. australis* and *H. anomalus*).

Despite its small and clumped known distribution, *Heteromys nubicolens* is likely widespread within the Cordillera de Tilarán and Cordillera de Guanacaste. Known localities are clustered in three well-sampled regions: one portion of the Cordillera de Tilarán (Monteverde/Peñas Blancas region) and two peaks in the Cordillera de Guanacaste (Cerro Cacao and Volcán Rincón de la Vieja–Volcán Santa María; fig. 4). Similar forested montane habitats also exist on Volcán Orosí (the northernmost volcano in Costa Rica, in the Cordillera de Guanacaste), Volcán Miravalles and Volcán Tenorio (which constitute the southern peaks of the Cordillera de Guanacaste), and throughout much of the Cordillera de Tilarán (i.e., in addition the Monteverde/Peñas Blancas region; Tosi, 1969). However, no specimens of *Heteromys nubicolens* are currently known from any of those areas. Until the late 1980s, the volcanoes of the Cordillera de Guanacaste received very little attention from mammalogists.[8] Even today, few specimens of mammals from this region reside in scientific collections. The mammalian faunas on Volcán Orosí, Volcán Miravalles, and Volcán Tenorio remain essentially unsampled. Similarly, the Monteverde/Peñas Blancas region represents the only high-elevation portion of the Cordillera de Tilarán that has seen significant sampling for mammals. Hence, we suspect that *H. nubicolens* is much more widely distributed within these two ranges than is documented by current records, and that the species' apparent absence from Volcán Orosí, Volcán Miravalles, and Volcán Tenorio (in the Cordillera de Guanacaste) as well as from many areas of the Cordillera de Tilarán is simply an artifact of inadequate sampling (see Anderson, 2003a for methods of testing such hypotheses).

Some of the known populations of *Heteromys nubicolens* are surely disjunct, being separated by lowland depressions (fig. 4). Given the elevational and ecogeographic tolerances mentioned above and the distribution of life zones in the region (Tosi, 1969), the populations on Cerro Cacao and on Volcán Rincón de la Vieja–Volcán Santa María are probably disjunct from each other and from other known populations of the species. Similarly, if the species exists on Volcán Miravalles or Volcán Tenorio, those populations are likely isolated as well. However, if the species inhabits Volcán Orosí, that population would likely be geographically continuous with the known population on Cerro Cacao, as these two neighboring peaks are linked by a saddle-like connection at ca. 1000 m. Similarly, any yet-undiscovered populations of the species in the Cordillera de Tilarán (which lacks significant lowland depressions) would likely be contiguous with documented populations in the Monteverde/Peñas Blancas region of that range. However, vegetational zones indicate that distributional areas for the species in the Cordillera de Tilarán are probably not contiguous with those in the Cordillera de Guanacaste. Given these interpretations, the low but significant level of morphological differentiation encountered between geographic samples from Monteverde and Cerro Cacao is not surprising (table 2; see Geographic Variation). Unfortunately, genetic comparisons are not currently available.

Climatic cycles associated with glacial and interglacial periods during the Pleistocene surely affected the species' distribution. Climatic and vegetational conditions during glacial periods likely allowed the species to inhabit lower elevations, whereas conditions in interglacial phases (similar to the present) may have led to retractions in its range (e.g., Colinvaux, 1996, 1997; Savage, 2002: 830). Niche-based distributional modeling using climatic and other environmental data in a Geographic Information Systems (GIS) environment can characterize a species' ecogeographic requirements and estimate its potential geographic distribution (e.g., Carpenter et al., 1993; Peterson, 2001; Anderson et al., 2002a; James and

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[8] Apparently, the first collection of the species now known as *Heteromys nubicolens* was in 1964 (from Monteverde; LACM 26121, 26175, 26179). The earliest known records of the species from the Cordillera de Guanacaste were collected in 1987 (Volcán Santa María; KU 158452; MNCR 789, 797) and 1988 (Cerro Cacao; KU 142775). See appendix 1 for full provenience.

McCulloch, 2002; Graham et al., 2004); projection of such models onto reconstructed past climates (cf. Peterson et al., 2002; Thomas et al., 2004) could shed light on the distributional history of *H. nubicolens*. Finally, combination of these approaches with phylogeographic and population-genetic analyses based on DNA sequences of rapidly evolving loci holds enormous promise for integrative evolutionary and biogeographic research (cf. Hugall et al., 2002). Clearly, however, such work must be preceded by thorough specimen-based alpha-taxonomic studies such as the present work.

Patterns of endemism remain poorly characterized in northwestern Costa Rica. The Monteverde region in the Cordillera de Tilarán is the best studied montane area in Costa Rica (Nadkarni and Wheelwright, 2000b). In contrast, the Cordillera de Guanacaste and the rest of the Cordillera de Tilarán have received little sampling by biologists (see above). The discrepancy in sampling between Monteverde versus other areas of northwestern Costa Rica (and other areas of the country) hinders considerations of endemism and renders any conclusions on the subject preliminary. Nevertheless, we summarize the following available information. We are not aware of general treatments of endemism in plants in the region, but ca. 10% of the plant species found at Monteverde are thought to be endemic to the Cordillera de Tilarán (Haber, 2000). Endemism appears lower in vertebrates. Presently, an undescribed species of *Reithrodontomys* represents the only mammal considered endemic to the Cordillera de Tilarán (Timm and LaVal, 2002a: 556–557, 2000b: 237); in contrast to *Heteromys nubicolens*, it has not been found in the Cordillera de Guanacaste. Four species of amphibians are thought to be endemic to the Cordillera de Tilarán or the Cordillera de Guanacaste. These include the salamanders *Nototriton gamezi* (known only from the Monteverde region of the Cordillera de Tilarán) and *Nototriton guanacaste* (from Cerro Cacao and Volcán Orosí in the Cordillera de Guanacaste), the recently extinct golden toad *Bufo periglenes* (which was found only in areas around Monteverde), and the frog *Eleutherodactylus cuaquero* (known only from Monteverde; Savage, 2002). No species of bird or reptile is deemed endemic to these ranges. However, one flycatcher (*Phainoptila melanoxantha*) has two subspecies: one (*P. m. parkeri*) is found only in the Cordillera de Tilarán and Cordillera de Guanacaste, and the other (*P. m. melanoxantha*) is widely distributed to the east (Barrantes and Sánchez, 2000). Even with terrestrial vertebrates, further sampling and systematic revisions of alpha-level taxonomy are necessary to allow for elucidation of detailed patterns of endemism in the complex region that comprises southern Central America.

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APPENDIX 1

GAZETTEER AND SPECIMENS EXAMINED IN PRINCIPAL STUDY AREA

Here we report all specimens of *Heteromys* examined from northwestern Costa Rica (northwest of the depression that separates the Cordillera de Tilarán from the Cordillera Central, and north of the crest of the Cordillera Central—see Museum Specimens). Secondary information deriving from sources other than the collector is included in brackets and, where applicable, is followed by the source. Where original elevation was reported in feet, we provide that datum as well as the metric equivalent to the nearest whole number. In addition to use of standard gazetteers and detailed topographic maps, R.M.T. returned to some collection localities and obtained global positioning system (GPS) readings. Localities are numbered to correspond to figure 4, where they are plotted, and are arranged here from north to south within provinces. For each entry, boldface type indicates the place name to which geographic coordinates correspond. We estimate that coordinates are accurate to within 5 km (ca. 2 minutes). Museum catalog numbers for specimens examined follow each locality, using the abbreviations provided in Materials and Methods. See appendix 2 for specimens examined outside the principal study area.

Heteromys desmarestianus (total 317)

COSTA RICA

ALAJUELA

1. Cantón Upala, Dos Ríos, **Finca La Selva**, 350 m [10°56′N, 85°20′W, IGCR, 1965], KU 158450, 158451; MNCR 792, 799; Cantón Upala, **Finca La Selva**, ca. 9 km NE Dos Ríos, 400 m [same coordinates], MNCR 795, 809.
2. Área de Conservación Guanacaste, **ca. 28 km NNE Liberia, San Cristóbal**, Río Cucaracha trail, 750 m [10°52′N, 85°23′W, IGCR, 1965; M. Klaus, personal commun.], KU 158499, 158500; Área de Conservación Guanacaste, **ca. 28 km NNE Liberia, San Cristóbal**, Sendero del Corredor, 370 m [same coordinates], KU 158501–158505; MNCR 1086, 1087.
3. Cantón Upala, Aguas Claras, **Colonia Libertad** [ca. 400 m; 10°51′N, 85°15′W, IGCR, 1965; N. Woodman, in litt.], MNCR 802, 805; Cantón Upala, Aguas Claras, **Colonia Libertad**, Finca Pérez [same coordinates], MNCR 796, 798; Cantón Upala, Aguas Claras, **Colonia Libertad**, Fila Cerro Chato, 750–800 m [same coordinates], MNCR 794.
4. Cantón Guatuso, Asentamiento **La Garroba**, 100–200 m [10°48′N, 84°55′W, IGCR, 1966a; N. Woodman, in litt.], KU 158876–158878.
5. Parque Nacional Rincón de la Vieja, **Quebrada Provisión**, 900–1000 m [10°47′N, 85°17′W, IGN, 1977; coordinates correspond to indicated elevation], KU 158547; MNCR 793, 806.
6. **San Carlos**, Buvart Farm, 800 ft [244 m; 10°33′N, 84°29′W, McPherson, 1985], FMNH 43994, 43995.
7. Bosque Eterno de los Niños, **Poco Sol**, Zambia trail, 750–800 m [10°21′N, 84°40′W, IGN, 1984; see also McCain, 2004], KU 160977, 160978.
8. **7 km (by road) NE Quesada**, 700 m [10°21′N, 84°24′W, IGN, 1986], LSUMZ 26357.

9. **Palmira de Zárcero**, 7000 ft [2134 m; 10°12′N, 84°22′W, IGCR, 1966c], FMNH 43993.
10. Volcán Poás, **Río Poasito**, 2000 m [10°10′N, 84°12′W, McPherson, 1985], UMMZ 123384, 123385.

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11. Área de Conservación Guanacaste, **ca. 39 km N Liberia, Pitilla** [ca. 700 m, 10°59′N, 85°26′W, IGCR, 1965; M. Klaus, personal commun.], KU 158512, 158513; MNCR 1088; Área de Conservación Guanacaste, **ca. 39 km N Liberia, Pitilla**, Sendero Carica [ca. 600–800 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158514; Área de Conservación Guanacaste, **ca. 39 km N Liberia, Pitilla**, Sendero Orosilito [ca. 700–900 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158506–158511; MNCR 1089.
12. Área de Conservación Guanacaste, **ca. 37 km NNW Liberia, Maritza**, Sendero Cacao [ca. 600–900 m, 10°57′N, 85°30′W, IGCR, 1965; M. Klaus, personal commun.], KU 158497, 158498.
13. Área de Conservación Guanacaste, **ca. 20 km NNE Liberia, Pailas**, Sendero Pailas, 800 m [10°47′N, 85°21′W, IGN, 1977; M. Klaus, personal commun.], KU 158607, 158608; Área de Conservación Guanacaste, **ca. 20 km NNE Liberia, Pailas**, Sendero Pailas, near Río Colorado, 800 m [same coordinates], KU 158614, 158615 (provisional identification only; see Sympatry and Zones of Contact with *Heteromys desmarestianus*). See also locality 29 for specimens of *H. nubicolens* from the same locality.
14. **Hacienda Santa María**; 18 mi E of Liberia [3200 ft (975 m), Goodwin, 1946; = 15 airline km NE of Liberia; 10°46′N, 85°19′W, McPherson, 1985; see also Harris, 1943], UMMZ 65221–65223.
15. **5 mi E, 2 mi S Tilarán** [780 m, 10°29′N, 84°54′W, IGN, 1982], LSUMZ 15783–15785; **5 mi E, 2 mi S Tilarán, Finca Silencio**, 780 m, same coordinates], LSUMZ 15786, 15787.
16. **3.0–3.5 mi E Tilarán**, 825–950 m [10°29′N, 84°55′W, IGN, 1982], LSUMZ 9469–9473, 10505; **4.1–5.0 km NE (by road) Tilarán**, 650 m [same coordinates], MVZ 164828–164843.
17. **Tilarán** [460 m; 10°28′N, 84°58′W, IGN, 1982], LSUMZ 9908.

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18. Río Sarapiquí, **Puerto Viejo** [Bob Hunter's cabin; Emmet Hooper field notes], 300 ft [91 m; 10°28′N, 84°01′W, IGN, 1985], UMMZ 112065; **Puerto Viejo** [50 m, IGN, 1985; same coordinates], KU 84370.
19. **Finca La Selva** [= La Selva Biological Station; 50 m, 10°26′N, 84°01′W, IGN, 1985], UMMZ 124791–124990; **La Selva** [= La Selva Biological Station; 50 m, IGN, 1985; same coordinates], KU 134860–134862; **La Selva Biological Reserve**, 3 km S Puerto Viejo [= La Selva Biological Station; 50 m, IGN, 1985; same coordinates], KU 158623.
20. Parque Nacional Braulio Carrillo, **11 km S, 4.5 km W Puerto Viejo**, 280–369 m [10°22′N, 84°03′W, Timm et al., 1989], FMNH 128429, 128431–128433, 128448–128450; MNCR 800.
21. Parque Nacional Braulio Carrillo, **1 km S, 11.5 km E San Miguel**, 680–710 m [10°18′N, 84°05′W, Timm et al., 1989], FMNH 128434–128437, 128440, 128446, 128453, 128455–128458; KU 142373; MNCR 801.
22. Parque Nacional Braulio Carrillo, **3.5 km S, 11.5 km E San Miguel**, 1000 m [10°17′N, 84°05′W, Timm et al., 1989], FMNH 128438, 128439, 128441, 128442, 128447.
23. Parque Nacional Braulio Carrillo, **9 km S, 11.5 km E San Miguel**, 1520 m [10°14′N, 84°05′W, Timm et al., 1989], FMNH 128443–128445.

Heteromys nubicolens (total 84)

COSTA RICA

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24. Monteverde, Monteverde Cloud Forest Reserve, **Peñas Blancas Valley**, Sendero Ticodendron below Refugio Eladios, 750–800 m [10°19′N, 84°43′W; IGCR, 1966d; coordinates correspond to indicated elevation; see also McCain, 2004], KU 159105, 159106.
25. Monteverde, Monteverde Cloud Forest Reserve, **Camino a Peñas Blancas**, 1000–1050 m [10°18′N, 84°46′W; IGCR, 1966b; coordinates correspond to indicated elevation; see also McCain, 2004], KU 159104.
26. Monteverde, Monteverde Cloud Forest Reserve, **Camino a Peñas Blancas**, 1250–1300 m [10°18′N, 84°47′W; IGCR, 1966b; coordinates correspond to indicated elevation; see also McCain, 2004], KU 159102, 159103.

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27. Rincón de la Vieja National Park, **Volcán Santa María, SE side**, 1100 m [10°47′N, 85°18′W, IGN, 1977; N. Woodman, personal commun.;

coordinates correspond to indicated elevation], KU 158452; MNCR 789, 797.

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28. Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao** [= Estación Mengo; 1100 m, 10°56′N, 85°28′W, IGCR, 1965; M. Klaus, personal commun.], KU 158515–158518; MNCR 1084; Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao**, Río Arenales [ca. 1100–1500 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158523; Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao**, Sendero al claro [ca. 1100–1500 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158520; MNCR 1085; Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao**, Sendero Cima del volcán [1200–1500 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158519; Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao**, Sendero Circular [ca. 1100–1500 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158522, 158526; Área de Conservación Guanacaste, **ca. 34 km NNW Liberia, [Cerro] Cacao**, Sendero Toma de agua [ca. 1100–1500 m, IGCR, 1965; M. Klaus, personal commun.; same coordinates], KU 158521, 158524, 158525; **SW side Volcán [= Cerro] Cacao, Estación Mengo**, 1100 m [same coordinates], KU 142775.
29. Área de Conservación Guanacaste, **ca. 20 km NNE Liberia, Pailas**, Sendero Cráter, 1200 m [10°47′N, 85°21′W, IGN, 1977; M. Klaus, personal commun.], KU 158609–158613; Área de Conservación Guanacaste, **ca. 20 km NNE Liberia, Pailas**, Sendero Pailas, near Río Colorado, 800 m [same coordinates], MNCR 1102; UCR uncataloged, field number MKACG 00-109. See also locality 13 for specimens of *H. desmarestianus* from the same locality.

PUNTARENAS

30. Monteverde, **Monteverde Cloud Forest Reserve, Cerro Amigos**, 1800–1840 m [10°19′N, 84°48′W, GPS reading; see also McCain, 2004], KU 159101; Monteverde, **Cerro Amigos**, 1790 m [same coordinates], KU 142057, 143455.
31. **Monteverde**, 1380 m [10°18′N, 84°49′W, GPS reading], LACM 26121; **Monteverde, Quebrada Moquina** [1450 m, IGCR, 1966b; same coordinates], KU 143456; **Monteverde, Quebrada Quecha** [1450 m, IGCR, 1966b; same coordinates], KU 143337; **Monteverde, Stella Wallace's house** [1400 m, IGCR, 1966b; same coordinates], KU 143339; **Monteverde, Stuckey lower woods** [1400–1420, Anderson, 1982; same coordinates], LACM 67450; **Monteverde, W. Guindon's property** [1450 m, IGCR, 1966b; same coordinates], UMMZ 116940; **Monteverde, William Haber's property**, 1350 m [same coordinates], FMNH 128428.
32. **Monteverde**, 1450 m [10°18′N, 84°48′W, GPS reading], KU 160202; LACM 26175, 26179; ROM 97307; **Monteverde**, 1500 m [same coordinates], KU 134857; **Monteverde** [ca. 1450–1500 m, IGCR, 1966b; same coordinates], KU 158321, 158322; LACM 64862; Monteverde, **Monteverde Cloud Forest Reserve, Investigator's Trail**, 1550 m [same coordinates; see also McCain, 2004], KU 159022–159029; MNCR 1336; **Monteverde, Arthur Rockwell's cafetales**, 1400 m [same coordinates], UMMZ 115419, 115420; **Monteverde, Hoge woods**, 1420 m [same coordinates], LACM 64867; **Monteverde, John Campbell's woods**, 1520–1580 m [same coordinates], FMNH 128417–128427; KU 142791, 143338; LACM 64861, 64863–64866, 64868, 67448; MNCR 803, 804; MVZ 161224, 161225.

APPENDIX 2

Other Specimens Examined (Outside Principal Study Area)

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

***Heteromys anomalus* (total 30): COLOMBIA (13):** Cundinamarca: Caparrapí, Volcanes, ICN 409, 1827–1831, 1832 (holotype of *Heteromys anomalus hershkovitzi*), 1833–1835, 1866; magdalena: below Minca, 1000 feet [305 m], AMNH 15347 (holotype of *Heteromys jesupi*), 15348. **TRINIDAD AND TOBAGO (7):** Trinidad: no specific locality [but see Thompson, 1815], BM(NH) 12.a (holotype of *Mus anomalus*); Caura, AMNH 7567/5960, 7575/5967, 7578/5970, 7588/5979, 7589/5980, 7594/5985. **VENEZUELA (10):** Zulia: Río Aurare, FMNH 18622, 18623 (holotype of *Heteromys anomalus brachialis*), 18624–18627; Unknown state: no specific locality, BM(NH) 47.2.1.4 (lectotype of *Heteromys melanoleucus*), 47.2.1.5 (lectoparatype of *Perognathus bicolor*), 47.2.1.6 (lectoparatype of *Heteromys melanoleucus*), 47.2.1.7 (lectotype of *Perognathus bicolor*). See Anderson (2003b) for additional specimens from Colombia, Venezuela, and Trinidad and Tobago.

***Heteromys australis* (total 27): COLOMBIA (1):** Valle del Cauca: Las Lomitas, 5000 ft [1524 m], AMNH 32240 (holotype of *Heteromys lomitensis*). **ECUADOR (10):** Esmeraldas: San Javier [= San Javier de Cachaví], 60–120 ft [18–37 m], BM(NH) 1.3.19.19, 1.3.19.20, 1.3.19.21, 1.3.19.22, 1.3.19.23 (holotype of *Heteromys australis*), 1.3.19.24; USNM 113304–13307. **PANAMA (16):** Darién: ca. 6 km NW Cana, E. slope Cerro Pirre, 1200 m, LSUMZ 25452; Cana, 1800–2000 ft [549–610 m], USNM 178621, 178698, 178699 (holotype of *Heteromys australis consicus*), 178700, 179595; Amagal, 1000–2000 ft [305–610 m], ANSP 19491–19498, 19499 (holotype of *Heteromys australis pacificus*), 19779. See Anderson (1999) for additional specimens from Colombia, Panama, and Venezuela; and Anderson and Jarrín-V. (2002) for additional individuals from Ecuador.

***Heteromys desmarestianus* (species complex; total 122): COSTA RICA (41):** Cartago: Angostura, USNM 12903/38590, 12904/38591 (holotype of *Heteromys desmarestianus subaffinis*), 12905/36848; Río Reventazón, 5.6 km SE (by road) Turrialba, 450 m, MVZ 164823–164827; Limón: 4.6 km W (by road) Limón, 25 m, MVZ 164844–164851; Puntarenas: 1.1 km SE (by road) Ciudad Nielly, 25 m, MVZ 164852–164857, 164865; San José: 4 km S, 2 km E Ojo de Agua, 2535 m, FMNH 128459; 16.3 km SE (by road) San Isidro, 525 m, MVZ 164858, 164859; Escazú, 3000 ft [914 m], AMNH 131729 (holotype of *Heteromys desmarestianus underwoodi*); Escazú, Los Higuerones, AMNH 137299–137302; Fila la Máquina, ca. 7.5 km E El Canaan, 8700 ft [2652 m], LSUMZ 13132–13138; San Gerónimo Pirris, USNM 250348 (holotype of *Heteromys desmarestianus planifrons*), 250349, 256445. **EL SALVADOR: (8):** Chalatenango: Los Esesmiles, 8000 ft [2439 m], MVZ 131116, 131117, 131119, 131121–131124, 131126 (paratypes of *Heteromys desmarestianus psakastus*). **GUATEMALA (1):** Alta Verapaz: Cobán, BM(NH) 43.6.13.1 (holotype of *Heteromys desmarestianus*). **MEXICO (23):** Chiapas: Chicharras, USNM 77576 (holotype of *Heteromys goldmani*), 77577, 77579–77582, 77694; Mountains near Tonala, USNM 76062 (holotype of *Heteromys griseus*), 76063–76070; Oaxaca: Mountains near Santo Domingo, USNM 73381, 73382 (holotype of *Heteromys goldmani lepturus*); Tehuantepec, Mazatlán, AMNH 165995 (holotype of *Heteromys nigricaudatus*); Veracruz: Motzorongo, USNM 63718, 63719 (holotype of *Heteromys temporalis*), 63720; Unknown State: no specific locality, BM(NH) 56.8.1.13 (holotype of *Heteromys longicaudatus*). **NICARAGUA (1):** Matagalpa: Tuma, AMNH 28451 (holotype of *Heteromys fuscatus*). **PANAMA (48):** Colón: Río Indio, near Gatún, USNM 170919, 170920, 170975, 170976 (holotype of *Heteromys zonalis*); Chiriquí: Boquete, 4000–5800 ft [1219–1768 m], MCZ B10355, B10356 (holotype of *Heteromys repens*), B10358, B10360, B10361; Cerro Pando, ANSP 17835 (holotype of *Heteromys desmarestianus chiriquensis*), 17836, 17837, 18374–18377; Darién: ca. 6 km NW Cana, E. slope Cerro Pirre, 1400 m, LSUMZ 25450, 25451; ca. 7 km NW Cana, E. slope Cerro Pirre, 1500 m, LSUMZ 25449, 25453, 25454; Mount Pirri [= Cerro Pirre], near head of Río Limón, 4500–5200 ft [1372–1585 m], USNM 178998–179004, 179006–179015, 179016 (holotype of *Heteromys crassirostris*), 179018–179020; Panamá: Cerro Azul, 2500–3000 ft [762–914 m], USNM 171107 (holotype of *Heteromys panamensis*), 171108–171111, 171128. See Anderson (1999) for additional specimens of *H. desmarestianus crassirostris* from Colombia and Panama.

***Heteromys gaumeri* (total 7): MEXICO (7):** Yucatán: Chichenitza [= Chichén Itzá], AMNH 12025/10458, 12027/10460, 12028/10461 (holotype of *Heteromys gaumeri*), 12029/10462, 12030/10463, 12031/10464; BM(NH) 97.4.5.3.

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

***Heteromys oasicus* (total 7): VENEZUELA:** Falcón: 49 km N, 32 km W of Coro, Cerro Santa

Ana [= 15 km SSW Pueblo Nuevo], 550–615 m, EBRG 15110, 15111; USNM 456325 (holotype of *Heteromys oasicus*), 456327, 495338; Cerro Santa Ana, Península de Paraguaná, 420–550 m, EBRG 3705, 15984. See Anderson (2003b) for additional specimens from Venezuela.

Heteromys oresterus **(total 17): COSTA RICA (17): CARTAGO**: El Muñeco (Río Navarro), 10 mi S of Cartago [= ca. 8 km S Cartago; McPherson, 1985], 4300 ft [1311 m], UMMZ 67306; **SAN JOSÉ**: El Copey de Dota, 6000–6500 ft [1829–1981 m], UMMZ 64026–64034, 66478; 2.2 km E (by road) La Trinidad de Dota, 2600 m, MVZ 164860–164864, 165786.

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