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A New Species of Spiny Pocket Mouse (Heteromyidae: *Heteromys*) Endemic to Western Ecuador

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ABSTRACT

Whereas previous treatments have considered *Heteromys australis* the only spiny pocket mouse present in Ecuador, morphological and morphometric analyses of specimens from Ecuador and southwestern Colombia reveal the presence of two species of the genus. *Heteromys australis* is distributed in evergreen forests from eastern Panamá and western Venezuela through Colombia to extreme northwestern Ecuador, where it inhabits wet, unseasonal areas of the Chocó and adjacent western slopes of the Andes. We here describe a new species, *Heteromys teleus*, found only in evergreen forests of central-western Ecuador, in areas less mesic and more seasonal than those characteristic of *H. australis*. Both species possess dark gray dorsal pelage, but *H. teleus* differs by larger (nonoverlapping) measurements of the hind foot and distinctive cranial proportions. Most notably, the rostrum of the new species is strikingly wide and massive, and the interparietal is narrow and rounded (in contrast to the wide, diamond-shaped interparietal of *H. australis*). The ranges of the two species together conform to the previously recognized Chocoan evergreen-forest fauna of western Colombia and northwestern Ecuador. However, the restriction of *H. teleus* to evergreen but seasonal forests of the southern Chocó (transitional between the relatively unseasonal evergreen forests of the central Chocó to the north and highly seasonal xeric regions to the south) is unique within currently

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recognized species of mammals. Biogeographic overviews hint at similar patterns in other groups, but more alpha-taxonomic research is necessary to evaluate mammalian distributional patterns in the region properly. Most suitable habitat for *H. teleus* has been converted to agricultural uses, and its current distribution is likely restricted to a handful of small-to-medium-sized forest patches.

RESUMEN

Mientras que estudios previos han considerado a *Heteromys australis* como el único ratón de abazones (= ratón bolsero; ratón bolsón; ratón mochilero) presente en Ecuador, análisis morfológicos y morfométricos de ejemplares provenientes de este país y del suroccidente de Colombia revelan la presencia de dos especies del género. *Heteromys australis* está distribuido en bosques siempreverdes, desde el este de Panamá y occidente de Venezuela, a través de Colombia, hasta el extremo noroccidental de Ecuador, donde habita áreas húmedas y sin estacionalidad del Chocó y estribaciones occidentales de los Andes. En el presente trabajo se describe una nueva especie, *Heteromys teleus*, hallada solamente en bosques siempreverdes de la región centro-occidental del Ecuador, en áreas menos húmedas y más estacionales que aquellas características para *H. australis*. Las dos especies poseen un pelaje dorsal de coloración grisácea oscura, pero *H. teleus* se caracteriza por tener mayores medidas (sin sobrelapamiento) de la longitud de la pata trasera y proporciones craneales distintivas. Más notoriamente, el rostro de la nueva especie es particularmente más ancho y robusto, y el interparietal angosto y redondeado (contrastando con el interparietal ancho y en forma de diamante de *H. australis*). Las distribuciones de las dos especies juntas se ajustan a la previamente aceptada fauna de los bosques siempreverdes del Chocó en el occidente de Colombia y el noroccidente del Ecuador. Sin embargo, la distribución de *H. teleus* es única entre las especies conocidas de mamíferos, estando restringida a bosques siempreverdes, pero con marcada estacionalidad, en el sur del Chocó (transicionales entre los bosques siempreverdes de poca estacionalidad del Chocó central al norte y las regiones áridas, fuertemente estacionales hacia el sur). Revisiones biogeográficas sugieren patrones similares para otros grupos, pero más investigación de la taxonomía alfa es necesaria para evaluar adecuadamente los patrones de distribución de los mamíferos en la región. La mayor parte del hábitat adecuado para *H. teleus* ha sido modificado para la agricultura, y su distribución actual probablemente está restringida a unos pocos parches de vegetación original de extensions relativamente pequeñas o medianas.

INTRODUCTION

The lowland faunas of the mesic Chocó and the xeric Tumbes regions come into contact west of the Andes in Ecuador (Chapman, 1926; Albuja-V. et al., 1980; Cracraft, 1985; Best and Kessler, 1995). This faunal turnover corresponds to a rapid and relatively uniform decrease in precipitation from north to south due primarily to the influence of the cold Humboldt Current in the south (Chapman, 1926; Lynch and Duellman, 1997; Cerón et al., 1999). Evergreen forests of western Ecuador belong to the Chocó, whereas deciduous (‘‘dry’’) forests and xeric, nonforested areas to the south comprise the Tumbes region (Cracraft, 1985). The distributions of many mammalian groups typical of lowland Neotropical rainforests terminate west of the Andes in this region (Emmons, 1997; Tirira-S., 1999). Furthermore, several clades present in rainforests west of the Andes (trans-Andean) in Central America and western Colombia encounter their southernmost distributions in western Ecuador and are not found in Amazonian forests to the east (e.g., *Diplomys*, *Heteromys*, *Hoplomys*, and *Tylomys*; Hershkovitz, 1972; Emmons, 1997). We here consider *Heteromys*, which shows a unique biogeographic history and has been used in several recent geographic studies (Anderson, 1999; Anderson and Soriano, 1999; Anderson et al., 2002a, 2002b).

The family Heteromyidae originated in North America, and three extant subfamilies are recognized: Dipodomyinae (kangaroo rats and kangaroo mice), Perognathinae (silky pocket mice), and Heteromyinae (spiny pocket mice). While the Dipodomyinae and Perognathinae have long fossil records in North America (Wood, 1935), members of the subfamily Heteromyinae show only Recent and Pleistocene records (Wahlert, 1993, removed the extinct genera *Proheteromys, Diprionomys,* and *Peridiomys* from the Heteromyinae). Despite this lack of fossil sequence, heteromyines comprise a well-defined monophyletic group distinct from either of the two other living subfamilies (Hafner, 1981; Hafner and Hafner, 1983; Wahlert, 1991).

Two genera exist in the subfamily Heteromyinae (*Heteromys* and *Liomys*), and their constituent species range latitudinally from extreme southern Texas (United States) to Ecuador. Within *Heteromys*, six (Williams et al., 1993) or seven (Patton, 1993) species are currently recognized, although more probably exist (Handley, 1976; Rogers, 1990; Anderson, 1999). Members of the genus *Heteromys* constitute the only heteromyids to have dispersed to South America (Hershkovitz, 1972; Simpson, 1980), and the timing and number of colonization events remain controversial (Anderson and Soriano, 1999; Anderson et al., 2002a).

In South America, *Heteromys* is restricted to the northwestern reaches of the continent, where two species are known to be widely distributed and one has a marginal range. *Heteromys anomalus* is found in deciduous and moderately mesic evergreen tropical forests across the Caribbean coast and northern foothills of Colombia and Venezuela, as well as on the islands of Margarita, Trinidad, and Tobago (Handley, 1976; Williams et al., 1993; Anderson, 1999) and from relatively xeric regions of the upper Magdalena Valley in Colombia (Hernández-Camacho, 1956; Anderson, 1999). In contrast, *H. australis* inhabits very mesic rainforests in the Pacific (Chocoan) lowlands of Ecuador, Colombia, and eastern Panamá as well as mesic montane forests eastward in the Colombian Andes. It ranges from sea level to circa 2500 m in sufficiently wet areas (Anderson, 1999) and has also been reported from the Cordillera de Mérida in western Venezuela (Anderson and Soriano, 1999). In addition to these two widely distributed species, a member of the *H. desmarestianus* complex inhabits high elevations of the Serranía del Darién in extreme northwestern Colombia (provisionally referred to as *H. d. crassirostris* by Anderson, 1999).

Thus, recent works have considered *Heteromys australis* the only spiny pocket mouse present in Ecuador (Albuja-V., 1991; Patton, 1993; Williams et al., 1993; Emmons, 1997; Anderson, 1999; Eisenberg and Redford, 1999; Nowak, 1999; Tirira-S., 1999). Thomas (1901) described *H. australis* from San Javier, in the coastal lowlands of Esmeraldas province in northwestern Ecuador near the Colombian border. In the next 100 years, the only specimens of the genus reported from the country derived from the type locality and two additional sites in the northwestern part of the country (Bulim and Río Palenque Science Center; Anderson, 1999), and one locality in the central-western region (Jauneche; Albuja-V., 1992). Here we examine a much larger number of specimens from Ecuador and southwestern Colombia in order to reevaluate the morphological variation, distributional extent, and taxonomic status of the spiny pocket mice present in this region.

MATERIALS AND METHODS

MUSEUM SPECIMENS

We examined 58 specimens of *Heteromys* from Ecuador, including most known from that country (and all known to us in museums in Canada, Ecuador, and the United States). We compared the Ecuadorian specimens with available material of *H. australis* from southwestern Colombia and with representative samples of other recognized species in the genus, including the majority of extant holotypes. Locality information not provided by the collector appears in brackets. Where original elevation was reported in feet, we provide that datum as well as the metric equivalent to the nearest whole number. Localities in Ecuador and southwestern Colombia are detailed in the Gazetteer (appendix 1). Specimens examined (see appendix 2) are housed in the following museum collections (* denotes museums holding specimens from Ecuador): Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH*); Departamento de Ciencias Biológicas, Escuela Politécnica Nacional, Quito

(EPN*); Field Museum, Chicago (FMNH*); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ*); Museo Ecuatoriano de Ciencias Naturales, Quito (MECN*); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Royal Ontario Museum, Toronto (ROM*); United States National Museum of Natural History, Washington, D.C. (USNM*); Universidad del Valle, Cali (UV); University of Kansas Natural History Museum, Lawrence (KU*); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); and University of Wisconsin Zoological Museum, Madison (UWZM*).

We also searched for specimens of the genus from Ecuador in the following museums, but did not find any records: California Academy of Sciences; Carnegie Museum of Natural History; Florida Museum of Natural History, University of Florida; Louisiana State University Museum of Natural Science; Michigan State University Museum; Museum of Texas Tech University; Museum of Vertebrate Zoology, University of California, Berkeley; Natural History Museum of Los Angeles County; Texas Cooperative Wildlife Collection, Texas A&M University; and University of New Mexico Museum of Southwestern Biology.

We examined external and cranial morphological characters, making comparisons among specimens of approximately the same age. Specimens were assigned to age classes based on patterns of toothwear and molt, following Rogers and Schmidly (1982). Morphological nomenclature follows Wahlert (1985) and Anderson (1999). To assess the habitat requirements of the species in Ecuador, we used available published reports and attempted to contact all living collectors.

MEASUREMENTS

We here define and illustrate 11 standard cranial measurements for *Heteromys* (fig. 1). These linear distances generally follow Genoways (1973), but we add parietal breadth, modify nasal length, substitute squamosal breadth for mastoid breadth, and follow Rogers and Schmidly (1982) in replacing depth of braincase with skull depth. Also, we rename greatest length of skull and alter the wording of Genoways (1973) to unify a telegraphic style. This current suite of measurements better reflects the morphology of the genus *Heteromys* relative to its sister genus *Liomys*, for which the measurements of Genoways (1973) were originally designed. The nasal length and mastoid breadth of Anderson (1999) and Anderson and Soriano (1999) represent the nasal length and squamosal breadth presented here, not those of Genoways (1973).

We took these measurements on all available intact skulls to the nearest 0.01 mm with digital calipers (except specimens from the ICN and UV collections, which were measured to the nearest 0.1 mm). Only adult specimens (age classes 4–6) were used for statistical analyses (see below). External measurements and mass were copied from specimen tags, but measurements taken only to the nearest centimeter or half centimeter on two series collected from Nariño, Colombia, in 1912 were excluded. Because some specimens lacked hind foot measurements and others were taken by a variety of collectors (some of which did not include the claws), we verified hind foot measurements with digital calipers for Ecuadorian specimens with complete pedal elements in study skins or fluid-preserved specimens.

Occipitonasal length (ONL): greatest distance from anteriormost projection of nasal bones to posteriormost portion of occipital bone (= greatest skull length of Anderson [1999] and Anderson and Soriano [1999] and greatest length of skull of Genoways [1973]).

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

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

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

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

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

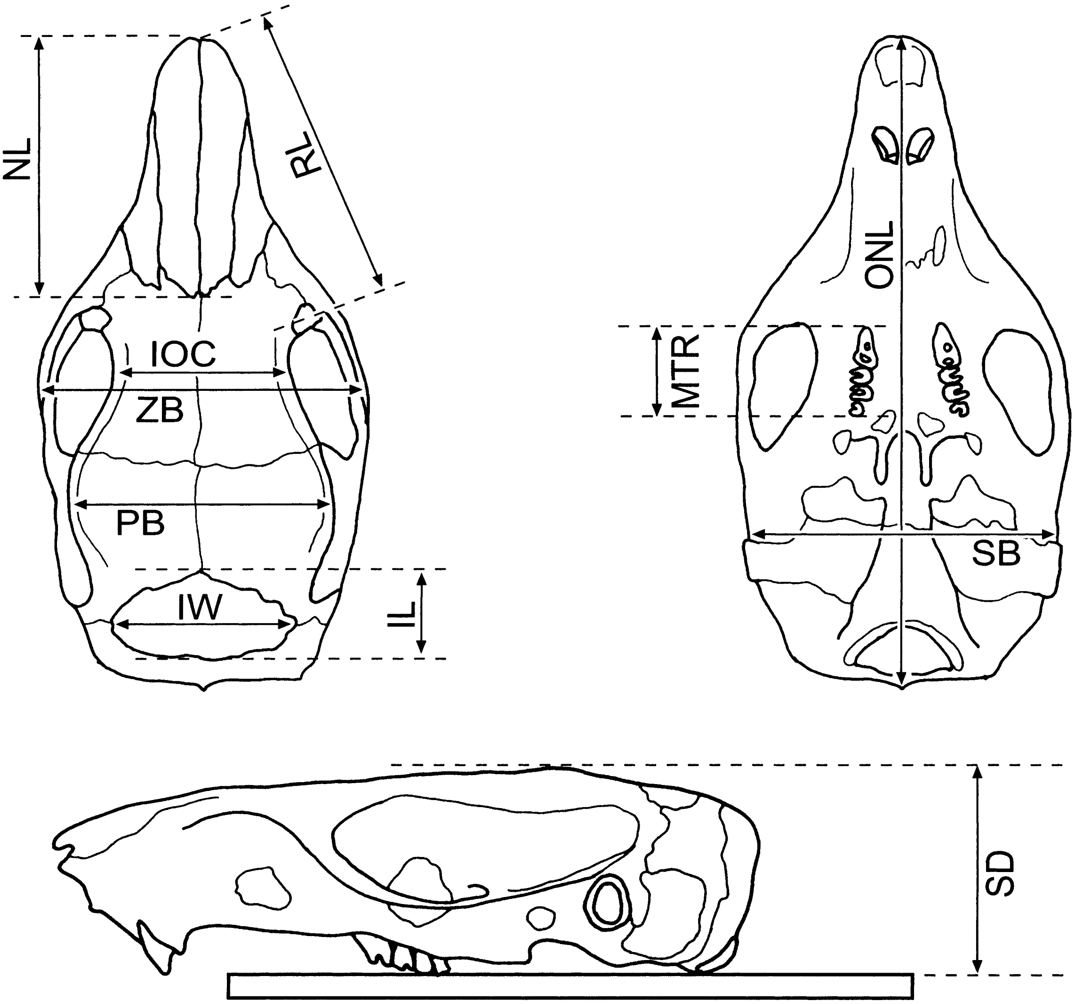

Fig. 1. Dorsal, ventral, and lateral views of a cranium of *Heteromys* showing method of taking measurements. Abbreviations and measurements are defined in the text.

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 width of slide).

STATISTICS

Specimens from Ecuador and southwestern Colombia were used for quantitative comparisons. Using species assignments based on our qualitative morphological examinations, we tested for sexual dimorphism in cranial measurements within a species in a series of univariate two-tailed *t*-tests of adult specimens in age class 4; based on those results, the sexes were pooled in all further analyses. For each species, we calculated descriptive statistics of adult specimens in age class 4 for: external measurements, mass, cranial measurements, and two derived ratios (tail length/head-and-body length and interparietal width/zygomatic breadth). All localities for each species were pooled because sample sizes were too small at individual sites. Additionally, we conducted two-tailed *t*-tests comparing means of the two species for each measurement or ratio.

We also conducted a principal components analysis (PCA) based on the variance-covariance matrix of $\log_e$-transformed cranial measurements of adult specimens in age classes 4–6. We interpreted the multivariate axes by examination of both loadings and coefficients (elements) of the unit eigenvector corresponding to each component. Loadings are Pearson product-moment correlations between specimen scores on an axis, and the respective $\log_e$-transformed measurements. We tested for differences between the species for scores on the first three principal components, by two-tailed *t*-tests. All statistical analyses were performed in Minitab (1998, version 12.1), and probabilities were compared to an α of 0.05 for hypothesis testing.

SYSTEMATICS

Our analyses indicate that two species of *Heteromys* are present in Ecuador. One species includes topotypes of *H. australis* and corresponds to the morphological diagnosis of that species (Anderson, 1999). The other species displays proportions and measurements distinct from those of *H. australis* as well as differences from all other recognized species of the genus. As no available name exists for it, we describe this taxon as:

Heteromys teleus, new species

Figure 2

HOLOTYPE: AMNH 64694, adult male; skin and skull in excellent condition; left and right rami of mandible separated. Collected on 2 June 1923 from Ecuador: Provincia Guayas: Cerro Manglar Alto, western slope by G.H.H. Tate; original number 1536. Tate's field camp was located at 1500 ft [457 m], but his notes and field catalog indicate that the holotype was taken at 2000 ft [610 m].

PARATYPES: We designate the following specimens (adult skins and skulls in good condition) from a variety of museum collections as paratypes. See also appendix 2 for other specimens not included in the type series (ICZN, 1999: article 72.4.6; recommendation 72B). ECUADOR (10): *Cotopaxi*: San Francisco de las Pampas, Reserva Bosque Nublado Otonga [= Bosque Integral Otonga], 1900–2000 m, QCAZ 1788. *Guayas*: Cerro Manglar Alto, eastern slope, Camp I, 1200 ft [366 m] (camp), specimen from 1400 ft [427 m], AMNH 64676; Cerro Manglar Alto, western slope, Camp II, 1500 ft [457 m] (camp), specimens from 2000 ft [610 m], AMNH 64681, 64682, 64686, 64689. *Los Ríos*: Río Palenque Biological Station [= Río Palenque Science Center], 220 m, KU 149133, 149135; Río Palenque Science Center, Santo Domingo, 47 km S of (by road), USNM 528573; Cantón Vinces, Parroquia Palenque, Jauneche, Estación Biológica Pedro Franco Dávila, 50 m, EPN 91.3038.

ETYMOLOGY: Latinized from the Greek *teleos*, meaning ‘‘having reached its end, finished, complete’’ (Brown 1956: 785) in reference to the species’ distribution at the southern end of the Chocó, representing the southernmost known distribution of the genus as well as of the superfamily Geomyoidea.

DISTRIBUTION: Known only from central-western Ecuador (fig. 3) from near the Río Esmeraldas and Río Guayllabamba (circa 0° 20′N) south to the Cordillera de Chongón-Colonche (southern extension of the Cordillera de la Costa; circa 1°47′S). Present from near sea level on the coastal plain to circa 2000 m on the western slopes of the Andes. Specimens from the Cordillera de Chongón-Colonche may be isolated from other populations, as this low cordillera lies in a matrix of drier vegetation (see Chapman, 1926; Foster, 1992b; Cerón et al., 1999; Sierra et al., 1999b). Note that some localities are documented only by specimens provisionally referred to the species (without examined cranial material) as listed in appendices 1 and 2.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following

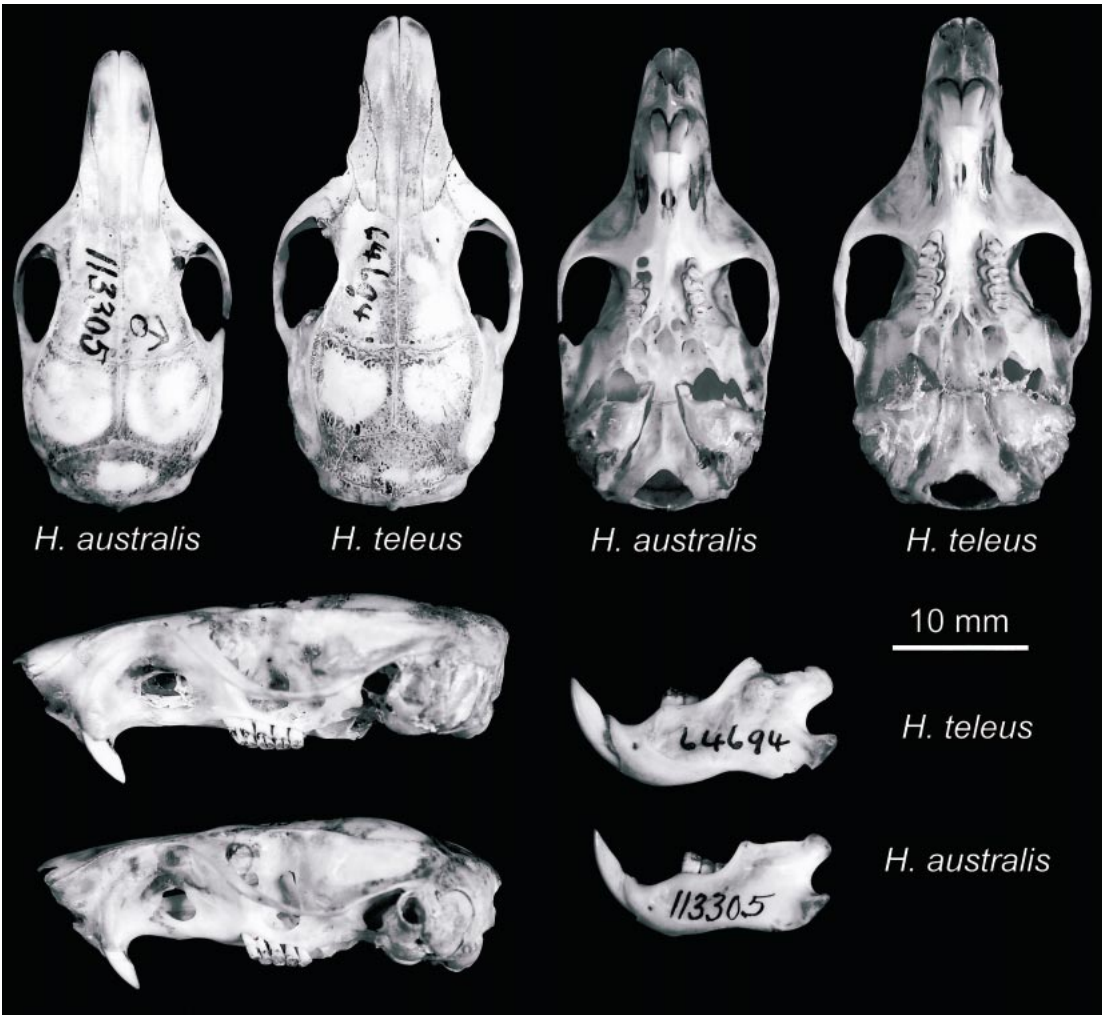

Fig. 2. Dorsal, ventral, and lateral views of the holotype of *Heteromys teleus* (AMNH 64694) and a topotype of *H. australis* (USNM 113305), both males in age class 4. Note the overall larger size and robustness of *H. teleus*, as well as its extremely wide rostrum and narrow interparietal.

combination of characters (fig. 2): mesopterygoid fossa V-shaped, with long, thin hamular processes of pterygoids; optic foramen small, with exterior margin formed by strong bar of bone; p4 with 3 lophs; skull large (ONL circa 35–38 mm in age class 4), robust, and wide (table 1); rostrum extremely wide, especially basal half; interparietal narrow and laterally rounded; molars distinctly wide; plantar surface of hind feet naked; dorsal pelage dark gray or blackish; no lateral ochraceous band present; pelage always harsh and spiny; ears small to medium in size; body size large, with hind foot 35 mm or greater in adults; tail (occasionally) approximately equal to or (more often) slightly longer than head-and-body length.

DESCRIPTION: Dorsal pelage spiny and dark gray or blackish, sharply contrasting with soft, pure-white pelage of venter (see illustration in Jarrín-V., 2001); ears blackish and small to medium in size (table 1); tail usually longer than head-and-body length (table 1) and moderately bicolored, with some dark hairs present on ventral surface, especially distally; hairs on dorsal surface of hind feet

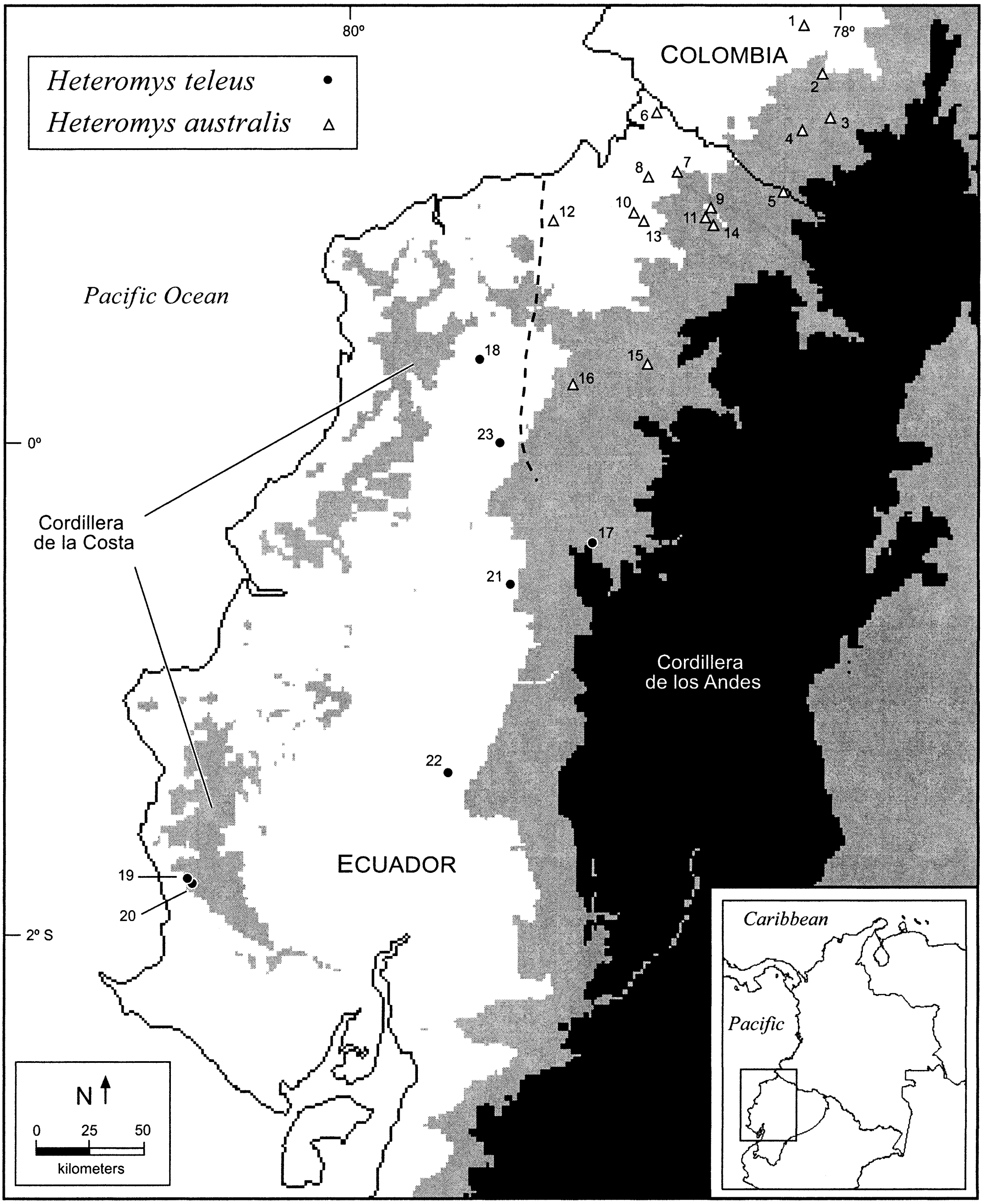

Fig. 3. Map showing collection localities for *Heteromys* in Ecuador and southwestern Colombia. Triangles represent localities of *Heteromys australis*, and circles denote localities of *H. teleus*. Localities are numbered to correspond to data given in appendix 1. Regions above 300 m are shown in gray shading, and areas above 2000 m appear in black. The dashed line in the northwestern part of the country denotes the division between coastal regions with a dry season more than 5 months long (southwest of the line) and areas with a shorter dry season (northeast of the line), adapted from Sierra et al. (1999b).

TABLE 1

Descriptive Statistics and Results of *t*-Tests Comparing Adults in Age Class 4 of *Heteromys australis* and *H. teleus* in Western Ecuador and Southwestern Colombia[a]

	H. australis	*H. teleus*
Total length**	254.9 ± 5.17, 14 (207–288)	279.7 ± 4.44, 10 (250–292)
Head-and-body length*	125.7 ± 2.56, 14 (108–145)	134.7 ± 1.98, 12 (121–148)
Tail length**	129.1 ± 3.22, 14 (95–143)	146.0 ± 3.74, 10 (124–161)
Tail/head-and-body ratio × 100 (%; n.s.)	102.9 ± 2.26, 14 (84.8–116.7)	109.3 ± 2.96, 10 (91.2–123.9)
Hind foot length****	31.8 ± 0.37, 14 (30–34)	37.7 ± 0.47, 14 (35–40)
Ear length (test not possible)	14.6 ± 0.41, 14 (11–16)	17.0, 1 (17)
Mass (grams; test not possible)	57.0 ± 3.11, 5 (49–68)	88.0, 1 (88)
Occipitonasal length****	34.4 ± 0.25, 14 (32.1–36.0)	37.1 ± 0.31, 11 (35.5–38.3)
Zygomatic breadth****	16.1 ± 0.17, 10 (14.9–16.8)	18.6 ± 0.23, 11 (17.3–19.8)
Rostral length***	15.0 ± 0.12, 14 (14.4–16.0)	16.4 ± 0.14, 12 (15.6–17.2)
Nasal length****	13.6 ± 0.17, 14 (12.9–14.9)	15.4 ± 0.15, 12 (14.4–16.4)
Least interorbital constriction**	8.9 ± 0.12, 16 (8.2–9.7)	9.4 ± 0.09, 12 (8.6–9.9)
Squamosal breadth****	14.8 ± 0.13, 15 (13.7–15.6)	16.2 ± 0.12, 11 (15.3–16.8)
Maxillary toothrow length****	5.3 ± 0.05, 16 (4.8–5.7)	6.0 ± 0.10, 12 (5.5–6.8)
Interparietal width***	9.7 ± 0.18, 16 (8.6–10.9)	8.8 ± 0.13, 11 (8.0–9.3)
Interparietal length*	5.1 ± 0.16, 16 (4.3–6.4)	5.5 ± 0.08, 12 (5.1–5.9)
Parietal breadth (n.s.)	13.3 ± 0.13, 16 (12.5–14.4)	13.4 ± 0.10, 12 (12.6–13.7)
Skull depth****	10.9 ± 0.09, 16 (10.4–11.6)	11.7 ± 0.08, 11 (11.2–12.1)
Interparietal width/zygomatic breadth ratio × 100 (%; ****)	59.6 ± 1.17, 10 (54.5–65.1)	47.0 ± 0.87, 11 (42.9–52.0)

[a] Mean ± standard error, sample size, and observed range (minimum–maximum) are given for each species. Measurements with significant differences in two-tailed comparisons between the species are indicated (* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; n.s. = $P > 0.05$). Sample sizes were too small to perform some tests. Note that some measurements do not overlap for the two species in this age class (e.g., hind foot length, zygomatic breadth), and that whereas averages of most measurements are larger for *H. teleus*, averages for interparietal width are larger in *H. australis*. In addition, no overlap occurs in the ratio of interparietal width to zygomatic breadth. Units are millimeters unless otherwise noted.

white, or white with moderate infusion of black hairs; hairs at base of claws of hind feet white; inner side of forearms white; hind feet large (table 1), with naked plantar surface; skull large (table 1) and robust (fig. 2); posterior half of premaxilla extremely wide, forming a distinctive shelf along dorsolateral border of rostrum; anterior roots of zygomatic arches robust; interorbital constriction moderately wide; braincase moderately wide with strong parietal crests, but not inflated; interparietal narrow (table 1) and rounded laterally; anterodorsal lobe of periotic capsule well developed, causing distinct undulation in posterior margin of squamosal (see schematic drawing in Anderson, 1999: 619); incisive foramina wide and bowed; molars large and wide; permanent upper premolar (P4) with short fold in anterior border of posterior loph; mesopterygoid fossa V-shaped, with hamular processes of pterygoids long and thin; optic foramen small, with exterior margin formed by strong bar of bone; jugular foramen (anterolateral to occipital condyle) large; p4 with 3 lophs.

DENTAL FORMULA: (incisors 1/1, canines 0/0, premolars 1/1; molars 3/3) × 2 = total 20.

MEASUREMENTS OF THE HOLOTYPE (mm): Total length 283, tail length 154, hind foot 37, ONL 36.44, ZB 18.68, RL 15.87, NL 15.30, IOC 8.59, SB 15.95, MTR 6.05, IW 8.01, IL 5.23, PB 12.61, SD 11.33.

COMPARISONS: The dark slaty-gray pelage of *Heteromys teleus* differentiates it from several species of the genus that have dorsal pelage strongly infused with brown or cinnamon (ochraceous) hairs, causing a grizzled effect. Among these, *H. gaumeri* and members of the *H. desmarestianus* complex (including *H. goldmani*; see Rogers, 1990, and Williams et al., 1993) inhabit Central America far from the known distribution of *H. teleus*. Specimens of *H. gaumeri* and many populations of the *H. desmarestianus* complex possess a lateral ochraceous band that is absent in *H. teleus*. Furthermore, *H. gaumeri* is much smaller than the new species (see Engstrom et al., 1987). Members of most populations of *H. anomalus* (from Colombia, Venezuela, and Trinidad and Tobago) have pale, especially grizzled pelage, in stark contrast to *H. teleus*. *Heteromys teleus* can be separated from all populations of *H. anomalus* by the narrower rostrum, relatively longer (usually sharply bicolored) tail, and larger, rounded ears of *H. anomalus*, as well as by differences in cranial proportions (relatively wider skull in *H. teleus* and narrower interorbit in *H. anomalus*).

When compared with other species of *Heteromys* that have dark pelage, *H. teleus* is easily distinguished by its extremely wide rostrum. *Heteromys oresterus* (endemic to the Cordillera de Talamanca in Costa Rica) has a characteristically long, thin rostrum. *Heteromys nelsoni* (distributed in southern México and western Guatemala) is even larger than the new species (Williams et al., 1993), with a more elongated skull (including rostrum), larger ears, dusky inner forearms, and soft dorsal pelage. The only other species of *Heteromys* with a similarly wide rostrum is a member of the *H. desmarestianus* complex present in the Darién region of eastern Panamá and northwestern Colombia (provisionally referred to as *H. d. crassirostris* in Anderson, 1999). That taxon, however, is one of the smallest of the genus (ONL 32.2–35.1 mm and hind foot length 29–34 mm in age classes 4–5; Anderson, 1999), has barely perceptible temporal fossae (erroneously named masseter-temporal fossae by Anderson, 1999), straight posterior margin of the squamosal, tapered incisive foramina, chocolate-brown dorsal pelage, and a relatively shorter tail.

Heteromys australis, which has a geographic range that probably comes into contact with that of *H. teleus* in northwestern Ecuador (or did historically; see appendices 1 and 2), merits closer comparisons. The two species are virtually indistinguishable externally (see below), but differ in cranial size and proportions. No sexual dimorphism was detected for any cranial measurement within either species (P = 0.18–0.98). In contrast, all raw measurements were significantly different between the two species (P ranges from < 0.0001 to 0.026 for significant comparisons; table 1) except for parietal breadth ($P = 0.71$). Generally, *H. teleus* is larger, but the interparietal width averages greater in *H. australis*. No overlap occurs between specimens (of any age class) of the two species in observed hind foot measurements (range = 35–40 mm for *H. teleus*, 29–34 mm for *H.*

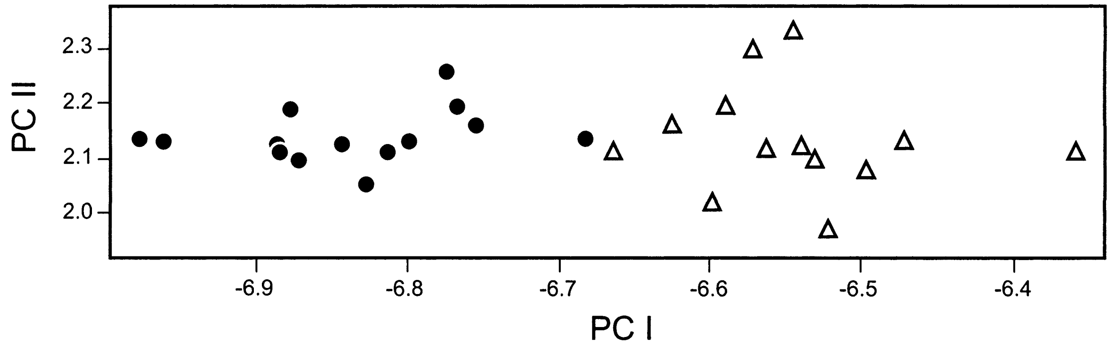

Fig. 4. Plot of specimen scores on PC I and PC II from a principal components analysis of log$_e$-transformed cranial measurements of adult specimens (age classes 4–6) of *Heteromys* from Ecuador and southwestern Colombia examined in this study. Triangles represent specimens of *H. australis*, and circles denote those of *H. teleus*. Axes are scaled relative to their eigenvalues (proportion of the variation explained).

australis), or for the derived ratio of interparietal width/zygomatic breadth (range = 0.423–0.520 for *H. teleus*, 0.555–0.689 for *H. australis*).

Multivariate analyses support the morphological distinctiveness of *Heteromys teleus* from *H. australis*. The two species separate clearly along the first principal component of the PCA undertaken on adult specimens (fig. 4), with no overlap between the two. The coefficients and loadings indicate that PC I represents a contrast between overall size and interparietal width (table 2). All measurements but interparietal width load negatively; thus, specimens with low scores on PC I (left portion of fig. 4) have relatively large values for all measurements except interparietal width. In contrast, specimens with high scores (right portion of fig. 4) hold small values for most measurements, but large ones

TABLE 2

Results of Principal Components Analysis of log$_e$-Transformed Cranial Measurements for Adult Specimens (Age Classes 4–6) of *Heteromys* from Ecuador and Southwestern Colombia Examined in This Study

(Elements of the unit eigenvectors, loadings, eigenvalues, and proportion of variance explained are given for each of the first three principal components.)

	Unit eigenvector			Loadings		
	PC I	PC II	PC III	PC I	PC II	PC III
ln-Occipitonasal length	−0.255	0.079	0.042	−0.941	0.134	0.065
ln-Zygomatic breadth	−0.422	0.156	−0.037	−0.949	0.160	−0.035
ln-Rostral length	−0.276	0.193	0.008	−0.905	0.289	0.011
ln-Nasal length	−0.367	0.239	−0.037	−0.861	0.256	−0.037
ln-Least interorbital constriction	−0.217	0.175	0.339	−0.648	0.239	0.427
ln-Squamosal breadth	−0.250	0.137	−0.002	−0.915	0.230	−0.003
ln-Maxillary toothrow length	−0.438	0.114	−0.048	−0.911	0.109	−0.042
ln-Interparietal width	0.216	0.178	0.846	0.496	0.187	0.822
ln-Interparietal length	−0.383	−0.877	0.243	−0.678	−0.710	0.182
ln-Parietal breadth	−0.100	0.020	0.300	−0.521	0.048	0.661
ln-Skull depth	−0.203	0.110	0.115	−0.841	0.209	0.202
Eigenvalue	**0.028**	**0.006**	**0.005**			
(% variation)	(63.8)	(13.3)	(11.4)			

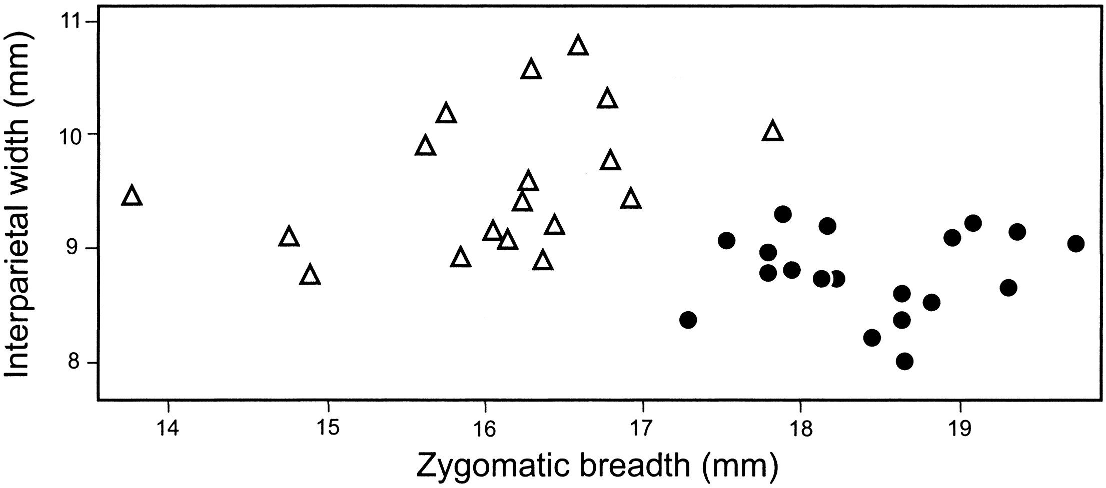

Fig. 5. Plot of interparietal width versus zygomatic breadth for all available specimens (age classes 2–6) of *Heteromys* from Ecuador and southwestern Colombia examined in this study. Triangles represent individuals of *H. australis*, and circles denote those of *H. teleus*. Although the two species overlap on either of the variables taken individually when considering specimens of various age classes (as here), the bivariate plot shows that specimens of *H. teleus* consistently have a narrower interparietal *relative* to the zygomatic breadth of the skull. Considering all age classes together, the two species do not overlap in the interparietal width/zygomatic breadth ratio.

for interparietal width. Species means were highly significantly different on PC I ($P < 0.0001$), but not on PC II or PC III ($P = 0.24–0.97$).

In sum, adults of *Heteromys teleus* show overall larger body size than *H. australis* and differ in cranial proportions. The hind foot is longer (nonoverlapping measurements regardless of age class) and the zygomatic breadth wider (nonoverlapping measurements for adults in age class 4; table 1). The rostrum is strikingly wider in *H. teleus*, both relatively and absolutely (although not measured), and the anterior roots of the zygomatic arches are more robust (fig. 2). In addition, the jugular foramina anterolateral to the occipital condyles are larger in *H. teleus*, and the molars are wider. Finally, regardless of age class, the interparietal is laterally rounded and relatively narrower in the new species, in contrast to the interparietal of *H. australis*, which is wide and flattened-diamond shaped (at least in this geographic region; figs. 2 and 5).

Both species possess dark gray dorsal pelage, but whereas the dorsal pelage of *Heteromys teleus* is always harsh and spiny, that of *H. australis* varies with altitude (spiny in lowlands, softer in highlands; see Anderson, 1999). The length of the hind foot represents the only reliable external character we know of for distinguishing the two species. Even the single available specimen of *H. teleus* in age class 1 has a larger hind foot (35 mm) than does any specimen of *H. australis* from Ecuador of any age class (the largest known specimens have a hind foot measuring 34 mm). Nevertheless, definitive identifications require collection of museum voucher specimens, given the difficulty of taking accurate hind foot measurements on live animals and the paucity of available specimens of the genus from Ecuadorian localities in museum collections.

NATURAL HISTORY: In contrast to some populations of *Heteromys* currently referred to *H. desmarestianus* in Central America (e.g., Fleming, 1970, 1974a, 1974b, 1977a, 1977b; Fleming and Brown, 1975; Vandermeer, 1979; Coates-Estrada and Estrada, 1988; Quintero and Sánchez-Cordero, 1989; Martínez-Gallardo and Sánchez-Cordero, 1993; Sánchez-Cordero, 1993; Sánchez-Cordero and Fleming, 1993; Brewer, 2001) or to *H. anomalus* in Venezuela (Pirlot, 1963; Rood, 1963; Rood and Test, 1968; Valdez et al., 1985), very little ecological information is available for the two species of *Heteromys* present in Ecuador (but see González-M. and Alberico [1993] for information on *H. australis* in western Colombia and Anderson [1999] for natural history information on *H. australis* gleaned from specimen tags and field notes). G.H.H. Tate offered in his field notes of 17 May 1923 at Cerro Manglar Alto this tantalizing report on the species that we now recognize as *H. teleus*: the *Heteromys* ‘‘use distinct runways, these are well worn and frequently placed about a foot below the top of the steep bank of the quebrada [= stream]. Every specimen but one [at eastern-slope camp] taken in quebrada, the other about 50 yards above in a cornfield. One specimen had a large cockroach in one cheek-pouch. Nocturnal.’’ On 21 May 1923 at the western camp, he added that the species ‘‘is probably distributed in the small watercourses throughout the region. It may be a water rat, but it is certainly a bank-rat, being almost always taken along the banks of the quebradas.’’ Another specimen had small seeds in its pouches.

DISCUSSION

ECOGEOGRAPHY

Within Ecuador, *Heteromys australis* inhabits areas wetter than the known localities of *H. teleus*. Whereas *H. australis* is restricted to the extreme northwestern portion of the country in very wet forests of the lowland Chocó and on the western versant of the Andes, *H. teleus* occupies slightly drier (but still evergreen) forests in the southernmost extension of the Chocó, also on the Pacific coastal plain and western slopes of the Andes (fig. 3; see also below and appendix 1). Both species inhabit a wide range of altitudes, from near sea level to approximately 2000 m (*H. teleus*) or to 1400 m (*H. australis*) in Ecuador, although the latter species is known to range up to circa 2500 m in parts of Colombia (Anderson, 1999). Lowland localities of *H. australis* in Ecuador are restricted to areas receiving more than 3000 mm of annual precipitation, but the two piedmont localities of that species lie in regions of between 2000 and 3000 mm of precipitation (IGM, 1995b). Such a shift in tolerances corresponds to lower potential evapotranspiration at higher (and thus cooler) elevations (Holdridge et al., 1971) and agrees with patterns for *H. australis* throughout the rest of its range (Anderson et al., 2002b). In contrast, northern localities of *H. teleus* hug the 3000-mm isopleth of annual precipitation, and southern ones enter regions receiving 1300–2000 mm of rainfall or even less (800–1300 mm for Cerro Manglar Alto; IGM, 1995b). However, the vegetation on the summits and high western slopes of this last site is nourished by ‘‘horizontal’’ precipitation in the form of mist and fog coming off the Pacific, making such areas functionally much more mesic than suggested by their direct precipitation (G.H.H. Tate field notes, 1923; see also Foster, 1992b, and Best and Kessler, 1995, for descriptions of similar sites).

This difference in absolute precipitation between collection localities of the two species correlates with seasonality of rainfall. Regions of Ecuador with over approximately 3000 mm in rainfall receive that precipitation relatively uniformly throughout the year (≤ 4 dry months; Sierra et al., 1999b) and are categorized as ‘‘húmedo tropical’’ in a broad scheme of climates and potential vegetation (IGM, 1995a). All localities of *Heteromys australis* in Ecuador correspond to this category. In contrast, areas receiving less rainfall in western Ecuador experience a strong dry season (IGM, 1995a, 1995b; Lynch and Duellman, 1997; see also Sierra et al., 1999a, 1999b). All but one locality of *H. teleus* fall into or very near areas of the ‘‘tropical monzón’’ category, with a pronounced dry season from June to November (IGM, 1995a). The one exception is Cerro Manglar Alto, which has a more stable climate due to coastal mists and fog. Hence, the macrogeographic distributions of these species in western Ecuador appear to correspond to climatic factors.

Current faunal and floral classifications of the region do not distinguish between areas corresponding to the respective distributions of *Heteromys australis* and *H. teleus*. Together, their distributions generally correspond to the ‘‘tropical noroccidental’’ and western ‘‘subtropical’’ zoogeographic regions of Albuja-V. et al. (1980; see also Albuja-V., 1999), the Colombian-Pacific Fauna of Chapman (1926), and the ‘‘humid tropical,'' ''humid subtropical,'' and ''subhumid tropical'' regimes of Lynch and Duellman (1997). However, the individual distributions of the two species do not coincide with demarcations within the former systems, or with categories in a recent classification of vegetation types in the country (Sierra et al., 1999b; see also supporting documentation in Sierra et al., 1999a). While Sierra et al. (1999b) recognized 46 vegetational formations, they did not make a distinction between the very wet, relatively unseasonal areas of evergreen forest where *H. australis* is found and the slightly drier, often highly seasonal (but still evergreen) regions characteristic of *H. teleus*. Both species have been collected in (or within 3 km of, given potential error in our geographic coordinates) regions classified as ''bosque siempreverde de tierras bajas,'' ''bosque siempreverde piemontano,'' and ''bosque simpreverde montano bajo.'' In addition, *H. teleus* also is documented from areas of ''bosque de neblina montano'' (Bosque Integral Otonga, the highest record for the species in the country) and ''bosque de neblina montano bajo'' (Cerro Manglar Alto, which is aberrantly mesic due to fog and mist off the ocean). This lack of predictive information regarding the individual species' distributions in these phytogeographic, zoogeographic, or bioclimatic classification systems highlights the value of an independent modeling approach for each species in faunal mapping projects (Peterson et al., 1999, 2002) rather than a vegetation-surrogate method.

CONSERVATION STATUS

Data provided by collectors indicate that both *Heteromys teleus* and *H. australis* have been captured in disturbed as well as primary forests (appendix 1). The disturbed forests vary in the forms of low-intensity human use, but they include systems that contain small cultivated plots, that are occasionally entered by free-ranging livestock, or from which wood has been selectively extracted by local inhabitants. No Ecuadorian collection locality of either species derives from a truly secondary site (recovering from being clearcut recently), deciduous forest, or open, nonforested area.

Six of the seven localities where *Heteromys teleus* has been collected now correspond to landscapes where most of the natural vegetation has been removed, and the other one (Bosque Integral Otonga) lies within 3 km of nonnatural vegetation (Sierra, 1999; our geographic coordinates have accuracy of approximately 3 km). Most of the original vegetation on the coastal plain of central-western Ecuador has been converted to agriculture, especially plantations of bananas and oil palms (Parker and Carr, 1992; Best and Kessler, 1995). Recent collections of *H. teleus* are from very small reserves containing relictual forest patches within the agricultural matrix (see appendices 1 and 2). As is typical elsewhere in the Neotropics, inventories of small mammals in Ecuador in past few decades have focused on areas of remaining natural or seminatural vegetation, and sampling effort for *H. teleus* in agricultural areas is inadequate. However, species of the genus *Heteromys* characteristically inhabit closed-canopy forests (Sánchez-Cordero and Fleming, 1993; Anderson, 1999), although *H. anomalus* also occurs in low-intensity or ''subsistence'' agricultural areas but not in high-intensity, large-scale industrial croplands (Anderson, 1999; Utrera et al., 2000). Hence, while the presence of *H. teleus* in areas of agricultural plantations in western Ecuador is unlikely, further collecting efforts are needed to establish the status of populations of native mammals there (emulating Cartaya and Aguilera, 1985; Martino and Aguilera, 1993; Utrera et al., 2000).

The long-term survival of *Heteromys teleus* in small, isolated forest remnants is unlikely (Harrison, 1991). Some larger tracts of forest remain along the western slope of the Andes (Sierra, 1999), but only one locality of the new species is from such high elevations (Bosque Integral Otonga). Among habitats that we consider typical for the species, the largest areas of intact forest probably lie in the Reserva Ecológica Mache-Chindul, which holds forest from near sea level to circa 700 m in the northern portion of the coastal cordillera (Sierra, 1999), but *H. teleus* has not yet been collected there. The other large protected area within the species' likely range is the Parque Nacional Machalilla, in the Cordillera de Chongón-Colonche (southern portion of the Cordillera de la Costa). However, much of this national park is deciduous forest not suitable for the species, and the park has been heavily logged and grazed by goats and cattle (L. Emmons, in litt. January 2002). In addition, all national parks and other governmentally protected areas in Ecuador face encroachment and various human uses, and the future of currently intact habitat at Mache-Chindul cannot be taken for granted. Like most rodents, no species of *Heteromys* was evaluated for the *Libro rojo de los mamíferos del Ecuador* (Tirira-S., 2001), but the limited range suggested by known localities indicates that *H. teleus* should be evaluated for potential listing.

In contrast, relatively large expanses of unseasonal wet forests remain in extreme northwestern Ecuador, in the range of *Heteromys australis* (Sierra, 1999). Because of extreme rainfall, these regions are not as suitable for agriculture, but timber is currently being exploited for large-scale industrial use (Parker and Carr, 1992; see also Best and Kessler, 1995). Seven of the 12 Ecuadorian localities of *H. australis* currently hold natural vegetation (Sierra, 1999), although they are within 3 km of areas converted to agriculture. The others lie in areas now deforested (Sierra, 1999), but which held forests at the dates of collection no more than 15 years ago (1987–1996; see appendix 1). The Reserva Cotacachi-Cayapas protects extensive premontane forests in northwestern Ecuador, but no large reserve exists in western Ecuador in unseasonal wet lowland rainforest. While expanses of suitable habitat remain in the Pacific lowlands of western Colombia (IAvH and Etter-R., 1998), little is protected in national parks (Garcés-Guerrero and De la Zerda-Lerner, 1994). Overall, the Andean distribution of *H. australis* has become highly fragmented by deforestation in the past 50 years, but its lowland distribution appears more intact (Anderson, 1999).

BIOGEOGRAPHY OF *HETEROMYS* IN SOUTH AMERICA

The occurrence of *Heteromys* only west of the Andes apparently results from the northern origin of the group and contingent, historical factors related to its subsequent colonization of South America (Hershkovitz, 1972; Anderson, 1999). The existence of 19 collection localities west of the Andes in Ecuador, with none known from the eastern slopes or Amazonian lowlands, makes the presence of any species of *Heteromys* east of the Andes in Ecuador unlikely. Albuja-V. (1999) presented a relatively uniform distribution of collection localities for bats east and west of the Andes in the country. Thus, because patterns of fieldwork for small rodents in the northern Neotropics are generally similar to those for bats, the genus' absence east of the Andes is not likely an artifact of biased sampling. Predictive models of the potential geographic distribution of *H. australis* indicated suitable environmental conditions for the species along both eastern and western flanks of the Andes in Ecuador (Anderson et al., 2002a). *Heteromys australis* is not known from the eastern slopes of the Andes in Colombia either, although the species has been recorded for the headwaters of the Río Magdalena near the crest of the Cordillera Oriental in southern Colombia. Its evident failure to cross this low pass, in seemingly suitable habitat, to colonize the eastern versant of the Andes of Colombia and Ecuador remains mysterious (Chapman, 1926: 44; Anderson, 1999; Anderson et al., 2002a).

Heteromys classically has been considered one of the latest North American groups to disperse to South America, with only a minimal level of differentiation on that continent (Hershkovitz, 1972; Simpson, 1980; Marshall et al., 1982; Webb, 1997). While pocket gophers (Geomyidae), which represent the sister group to heteromyids, have dispersed only to extreme northwestern South America west of the Río Atrato/Río San Juan lowlands or Bolívar Geosyncline (Alberico, 1990), heteromyids are distributed much more extensively (Handley, 1976; Anderson, 1999). Although the timing of their entry into South America is controversial, recent alpha-systematic (species-level) and geographic-modeling research has shown that *Heteromys* distributions in South America are more complex than previously recognized (Anderson, 1999; Anderson and Soriano, 1999; Anderson et al., 2002a). The present discovery of a new species endemic to western Ecuador adds a new level of complexity to the emerging understanding of the group's differentiation in South America. Evolutionary relationships among species of the genus remain unresolved (Rogers, 1990), but a phylogenetic study of the subfamily Heteromyinae using morphological characters is underway (Anderson, unpubl.). Furthermore, other undescribed species of *Heteromys* exist in South America (Handley, 1976; Anderson, 1999). Thus, an overall account of heteromyid diversity and evolution in South America is not yet possible.

FAUNAL RELATIONSHIPS AND ENDEMISM

Under various names, the faunal turnover in western Ecuador between Chocoan rainforest elements and Tumbesan species characteristic of southern xeric areas has been long established (Chapman, 1926; Albuja-V. et al., 1980; Cracraft, 1985). Many mammalian species characteristic of trans-Andean rainforests reach their southernmost geographic distribution in Ecuador west of the Andes (e.g., primates *Alouatta palliata* and *Cebus capuchinus*; rodents *Microsciurus mimulus* and *Oryzomys bolivaris*; and the bat *Rhinophylla alethina*; Emmons, 1997; Tirira-S., 1999). Most such trans-Andean rainforest species are closely related to Amazonian species in the same genus, and—at least following current taxonomy—many other rainforest species are found on both sides of the Andes (Emmons, 1997; Tirira-S., 1999). In contrast, *Heteromys* and *Tylomys* (naked-tailed climbing rats) represent the only mammalian clades of North American origin to reach their southern termination in western Ecuador (Hershkovitz, 1972; Tirira-S., 1999; note that *Reithrodontomys*, harvest mice, and *Cryptotis*, shrews, also represent diverse North American clades with marginal ranges in South America, but there they have Andean distributions that terminate in montane Ecuador and Peru, respectively; Hooper, 1952; Vivar et al., 1997).

Further, *Heteromys teleus* holds a unique position among mammals endemic to Ecuador. The overwhelming majority of Ecuadorian endemics are rodents, and *H. teleus* is the only one of them found on the western coastal plain. Among the 27 terrestrial mammals listed as endemic to the country by Tirira-S. (1999), most are montane (13; found only over 1000 m) or from the Galápagos islands (8). Two others (*Proechimys gularis* and *Oryzomys tatei*; rodents) are Amazonian, one is of unknown locality within the country (*Bolomys punctulatus*, a rodent; see Voss, 1991), and the remainder (3) are from west of the Andes. Of the three western species (all bats), one remains undescribed (*Sturnira* sp. A of Tirira-S., 1999), and one has since been reported for southwestern Colombia (*Balantiopteryx infusca*; Alberico et al., 2000; see also McCarthy et al., 2000). The last (*Cabreramops* [= *Molossops*] *aequatorianus*) is a rare, high-flying bat only known from two localities in central-western Ecuador (Ibáñez, 1980; Tirira-S., 1999: 138). That species' distribution and evolutionary history remain enigmatic, but it appears to inhabit areas drier than those typical of *H. teleus*, including deciduous forests where *H. teleus* is not known. Albuja-V. (1999) also mentioned undescribed species of the chiropteran genera *Lonchophylla* and *Sturnira* from extreme northwestern regions of the country, areas wetter than those inhabited by *H. teleus*. Hence, *H. teleus* may represent the only mammalian species restricted to seasonal evergreen forests of the southern Chocó. However, Emmons and Albuja (1992) mentioned the possible species-level status of a brocket deer (currently *Mazama americana fuscata*) and a white-fronted capuchin (currently *Cebus albifrons aequatorialis*) in central-western Ecuador. The taxonomic status of those forms has not yet been resolved, but they do show distributional patterns similar to that of *H. teleus*.

We know of no formalized faunal division within Ecuador corresponding to the distributions of *Heteromys australis* and *H. teleus*, but several studies hint that may be the case. Several authors have divided the Chocó into northern and southern faunal regions for mammals and herpetofauna, with the division present at approximately Buenaventura in central-western Colombia (e.g., Lynch, 1979; Hernández-Camacho et al., 1992). This division is much less marked than that recognized for birds between the Chocó and the Nechí region north of the Andes in Colombia (Cracraft, 1985). In contrast to these northern divisions for faunal groups, Gentry (1992: 57) was the first to recognize western Ecuador south of the town of Esmeraldas as a ‘‘unique and distinctive floristic region for wet and moist forest . . . rather than as the tail-end of the Chocó flora.’’ Although not formalized as a faunal division, distributional maps for rainforest lizards and snakes suggest a similar pattern (Dixon, 1979). Furthermore, Almendáriz and Carr (1992) state that 42% of the species of herpetofauna that they collected in western Ecuador were endemic to that region, including some species characteristic of moist forests.

Nevertheless, as mentioned by Emmons and Albuja (1992), Hernández-Camacho et al. (1992), Voss and Emmons (1996), and Cadena et al. (1998), vast regions of the Chocó remain unsampled or inadequately sampled, and taxonomic understanding of small mammals (and most other taxonomic groups) of this and other adjacent regions remains woefully incomplete. Thus, fine faunal divisions and analyses of endemism remain premature and dependent upon scattered and incomplete collection localities, as well as inadequate alpha-taxonomic work. Future inventories and comprehensive taxonomic revisions will undoubtedly bring to light currently unrecognized species and refine our understanding of the true distributional patterns of small mammals in the region, which in most cases can now only be imperfectly approximated.

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APPENDIX 1: Gazetteer

Collection localities for *Heteromys* in Ecuador and southwestern Colombia follow. Only abbreviated locality names are given here; see appendix 2 for full provenience and museum catalog numbers. Secondary political divisions (*Departamento, Provincia*) are italicized, and localities are arranged from N to S within secondary political divisions.

Heteromys australis

COLOMBIA

NARIÑO

1. Barbacoas [1°41′N, 78°09′W; 35 m; Paynter, 1997]. Collected by W.B. Richardson in August 1912. ‘‘Thick forest and impenetrable jungle’’ on Pacific coastal plain (Chapman, 1917: 641).
2. Buenavista [1°29′N, 78°05′W; Paynter, 1997], 1200 ft [366 m]. Collected by W.B. Richardson in September–October 1912. General area was ‘‘uncultivated and . . . inhabited [by humans] only along the road’’ Chapman (1917: 50), but condition of exact collection site unclear.
3. Reserva Natural del Río Ñambí [1°18′N, 78°03′W; Cadena et al., 1998], 1300 m. Collected by A. Cadena, P. Rivas-Pava, and R.P. Anderson in March 1995. Very wet primary premontane rainforest, with much fog, epiphytes, mosses, and palms (Cadena et al., 1998).
4. Planada de Maindés (Junín) [1°15′N, 78°10′W; Orejuela-Gartner et al., 1982], 870 m. Collected by M.S. Alberico in August 1981. Pluvial forest (transition between tropical and premontane) with moderate extraction of wood by locals; moss and orchids very common (Orejuela-Gartner et al., 1982).

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5. El Pailón [1°00′N, 78°14′W; Albuja-V., 1989, 1999], 1400 m (includes sublocalities). Collected by L. Albuja-V. and P. Mena-V. in November 1987. Disturbed forest (i.e., with some selective extraction of wood) in an area with strongly broken topography (Albuja-V., 1989; L. Albuja-V., personal commun. January 2001).

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6. Mataje [1°22′N, 78°43′W; 50 m; Albuja-V., 1999]. Collected by L. Albuja-V. and P. Mena-V. in October 1991. Disturbed forest (L. Albuja-V., personal commun. January 2001).
7. Bulim [= Pulún; 1°05′N, 78°40′W; Paynter, 1993], 160 ft [49 m]. Collected by W. Rosenberg in November 1900. Tropical zone of coastal plain at foot of mountains (Paynter, 1993). State of forest at time of collection unknown but likely quite intact.
8. San Javier [= San Javier de Cachaví; 1°04′N, 78°47′W; Paynter, 1993], 60–120 ft [18–37 m]. Collected by G. Flemming in May–June 1900. ‘‘Interior northern Esmeraldas on coastal plain, on railroad’’ (Paynter, 1993). State of forest at time of collection unknown, but likely intact away from railroad; exact site of collection unknown.
9. Alto Tambo [0°56′N, 78°32′W; 750 m; Tirira-S., 1999]. Collected by D. Tirira-S. in December 1990. Based only on adult fluid-preserved specimen with small hind foot; not confirmed by cranial material; but note other nearby localities. Caught in a handcrafted wooden trap used by local inhabitants to capture small rodents for food (see also Albuja-V. and Mena-V., 1987, for illustration of and Cadena et al., 1998, for mention of similar traps). Relatively pristine forest with low-intensity use by nearby human settlements at time of capture; the natural vegetation in this area was subsequently destroyed concomitant with the construction of the Ibarra-San Lorenzo highway (D. Tirira-S., in litt. August 2001).
10. Estero Zapote [0°55′N, 78°51′W for El Zapote; IGM, 1985]. At 190 m on ‘‘left bank of the Río Santiago approximately an

hour's journey in motorized canoe from Playa de Oro/Luis Vargas Torres'' (J. Cevallos, in litt. October 2001; translation ours). Collected by J. Cevallos in June 1993. Based only on adult study skin with small hind foot; not confirmed with cranial material; but note nearby localities. Trapline was situated in the upper parts of the swamp and included both mature forest and areas regenerating after recent agricultural uses; habitat type of capture area not available (J. Cevallos, in litt. October 2001).

11. Alto Tambo, 2 km S of (0°54′N, 78°33′W; collection tag), 700 m. Collected by B.K. Lim and F. Sornoza-Molina in March 1996. General area was disturbed humid forest (B.K. Lim, in litt. August 2001), but the *Heteromys* was captured on a downed log in a swampy area of otherwise well-drained primary forest, which was subsequently clearcut (F. Sornoza-Molina, in litt. October 2001).
12. Reserva La Mayronga [0°53′N, 79°10′W; L. Nolivos-D., in litt. February 2001; see also Lynch and Duellman, 1997]. Collected by G. Onore and A. Barragán-Yáñez in October 1993 and by L. Nolivos-D. and I. Castro in September–October 1998. Onore and Barragán-Yáñez captured the mice by hand after turning over fallen palm fronds (*Astrocaryum* sp.; common name *chambira*) in primary humid tropical forest (A. Barragán-Yáñez, in litt. October 2001). Several individuals were encountered each time a frond was disturbed, but only two *Heteromys* (both juveniles) were preserved as voucher specimens; thus it is not known whether adults were present there as well. Nuts of the same palm were present underneath the fronds. L. Nolivos-D. (in litt. February 2001) provided the following information on his and Castro's later fieldwork in the reserve: specimens were found in disturbed tropical forest (ENSOA management treatment ''Área Bajo Explotación Normal'') with irregular topography and a partially open canopy; two individuals were captured near a swampy area, and the other next to a *pambil* palm (*Iriartea deltoidea*).
13. Luis Vargas Torres [= Playa de Oro; 0°53′N, 78°48′W; 50 m; Albuja-V., 1989, 1999, but see Albuja-V. and Mena-V., 1987; not Tirira-S., 1999]. Collected by L. Albuja-V. in October 1994. Specimens were trapped in both primary forest farther from the town of Luis Vargas Torres and disturbed forest (which held some small plots of cultivars) closer to town (L. Albuja-V., personal commun. January 2001; see also Albuja-V. and Mena-V., 1987).
14. Hacienda La Granada [0°52′N, 78°31′W; Albuja-V., 1989, 1999], 670 m. Collected by L. Albuja-V. and P. Mena-V. in August 1994. Disturbed forest (L. Albuja-V., personal commun. January 2001) in an extremely wet area of highly irregular terrain (Albuja-V., 1989).

IMBABURA

15. Los Cedros [0°18′N, 78°47′W; IGM, 1973; Young-Owl et al., 1992], 1400–1450 m. Collected by M. Bronsvoort in August 1993. Based only on adult fluid-preserved specimen with small hind foot; not confirmed with cranial material. State of forest at time of collection unknown, but general region holds much intact forest (C. Carrión, personal commun. January 2001).

PICHINCHA

16. Salcedo Lindo [0°13′N, 79°05′W; circa 450 m; IGM, 1991]. Collected by R.E. Bleiweiss, F.A. Iwen, and F. Sornoza-Molina in November 1991. ''Trapped in forest; dense vegetation and downed logs'' (R.E. Bleiweiss field notes, November 1991); at the base of a tree in primary forest (F. Sornoza-Molina, in litt. October 2001).

Heteromys teleus

ECUADOR

COTOPAXI

17. Bosque Integral Otonga [0°25′S, 79°00′W; Freiberg, 1998 and Jarrín-V., 2001; not Lynch and Duellman, 1997 or Tirira-S., 1999], 1900–2000 m. Collected by P. Jarrín-V. in September 1996. Small reserve (1000 ha) of mainly primary premontane and montane wet tropical forest on the western slopes of the Andes, adjacent to larger protected areas (Jarrín-V., 2001). Canopy not completely closed; with ''a dense shrubby and herbaceous ground flora'' (Freiberg, 1998: 168). The *Heteromys* was caught at ground level in primary cloud forest, in an area with highly irregular terrain. See Moret (1991), Schätti and Kramer (1991, 1993), Coloma (1995), Kizirian (1996), Lynch and Duellman (1997),

and Jarrín-V. (2001) for other faunal reports.

ESMERALDAS

18. Quinindé [0°20′N, 79°28′W; 100 m; Albuja-V. and Mena-V., 1987; Albuja-V., 1999]. Collected by R. Rageot in October 1980. Based only on adult study skin with large hind foot; not confirmed by cranial material. Most of the region has been converted to cattle pastures and plantations of oil palms and bananas, but with remnant disturbed forests still present at least in 1971 (Albuja-V. and Mena-V., 1987; Lynch and Duellman, 1997). Habitat conditions at site of capture not available.

GUAYAS

19. Cerro Manglar Alto, eastern slope, [1°46′S, 80°38′W; IGM, 1989; G.H.H. Tate field notes, May 1923; not Voss, 1992 or Musser et al., 1998, who followed the coordinates given for the town of Manglar Alto by Paynter and Traylor, 1977 and Paynter, 1993, respectively], specimens from 1400 ft [427 m]. Collected by G.H.H. Tate in May 1923. See site 20 for general site information. A large cornfield and several small pastures lay in the immediate vicinity of this camp; the surrounding area was ‘‘dense, fairly dry, *tagua* [*Phytelephas aequatorialis*, a palm] jungle.’’ Specimens taken in stream bank running through forest and in nearby cornfield.
20. Cerro Manglar Alto, western slope [1°47′S, 80°37′W; IGM, 1989; G.H.H. Tate field notes, May 1923; not Voss, 1992 or Musser et al., 1998, who followed the coordinates given for the town of Manglar Alto by Paynter and Traylor, 1977 and Paynter, 1993, respectively], specimens from 2000 ft [610 m]. Collected by G.H.H. Tate in May–June 1923. Cerro Manglar Alto is the name used by Tate to refer to the portion of the Cordillera de Chongón-Colonche (southern extension of the Cordillera de la Costa) at the headwaters of the Río Manglar Alto (= Río Culebra) immediately east of the coastal town Manglar Alto. The low peaks in this region receive various names on detailed maps (IGM, 1988, 1989), but none of them is known as Cerro Manglar Alto. Nevertheless, consultation of Tate’s field notes and a detailed, modern map (IGM, 1989) allows for a fairly precise localization of his collecting sites and tentative assignment of coordinates, which we judge to be accurate to within a minute. Both of Tate’s camps apparently were located between the Cerro Las Mesas and the Loma Colonche, and near the crest of the cordillera (IGM, 1989). A general characterization of the region follows: ‘‘Dense, wet, *tagua* [*Phytelephas aequatorialis*, a palm] forest, which continues up to 1600 or 2000 ft [488–610 m] in the most westerly ridges of the range. Moisture [is] caught by these spurs leaving the rest of the hillcrest further east practically dry although just about as high’’ (G.H.H. Tate field notes, May 1923). Specimens from this camp on the western slopes were taken along the Río Domene (not found on our maps), a small tributary of the Río Manglar Alto/Río Culebra, in undisturbed forest. There, *Heteromys* was ‘‘only taken in traps placed in runways which passed immediately below the overhang of the bank in its steepest parts’’ (G.H.H. Tate field notes, May 1923).

LOS RÍOS

21. Río Palenque Science Center [0°34′S 79°20′W; Lynch and Duellman, 1997; see also Best and Kessler, 1995 and Albuja-V., 1999], 220 m. Collected by A.T. Smith in March 1977 and by D.E. Wilson in February 1979. Found in primary forest (A.T. Smith, in litt. August 2001); habitat information regarding the specimen collected by Wilson unknown. Now-isolated forest reserve containing both primary (87 ha) and secondary (80 ha) habitats (Paynter, 1993; see also Dodson and Gentry, 1978).
22. Jauneche (Estación Biológica Pedro Franco Dávila) [1°20′S 79°35′W; Albuja-V., 1992, 1999], 50 m. Collected by L. Albuja-V. in July 1991. Found in disturbed forest (L. Albuja-V., personal commun. January 2001). Reserve encompasses 138 ha (Best and Kessler, 1995); see also Dodson et al. (1985) and Foster (1992a) for botanical characterizations.

PICHINCHA

23. Bosque Protector La Perla [0°00′N, 79°23′W; Lynch and Duellman, 1997; not Tirira-S., 1999], 220 m. Collected by F. Campos-Y. in May 1990. Based only on adult study skin with large hind foot; not confirmed by cranial material. This reserve characterized as a ‘‘remnant of humid tropical rainforest’’ (Lynch and Duellman, 1997) surrounded by agricultural areas.

The *Heteromys* was captured in a disturbed, seasonally flooded forest (250 ha in area at the time) dominated by various species of palms (especially *Iriartea deltoidea*), with many downed trunks present. The forest has been selectively logged; this practice largely ceased with the creation of the reserve, but cattle continued to enter from the surrounding pastures in 1990 (F. Campos-Y., in litt. August 2001).

APPENDIX 2: Specimens Examined

***Heteromys anomalus* (25): COLOMBIA** (13): Cundinamarca: Caparrapí, Volcanes, ICN 409, 1827–1831, 1832 (holotype of *Heteromys anomalus hershkovitzi*), 1833–1835, 1866. Magdalena: below Minca, 1000 ft [305 m], AMNH 15347 (holotype of *Heteromys jesupi*), 15348. **TRINIDAD AND TOBAGO** (6): Trinidad: Caura, AMNH 7567/5960, 7575/5967, 7578/5970, 7588/5979, 7589/5980, 7594/5985. **VENEZUELA** (6): Zulia: Río Aurare, FMNH 18622, 18623 (holotype of *Heteromys anomalus brachialis*), 18624–18627. See also 64 other specimens from Venezuela reported in Anderson and Soriano (1999) and 201 from Colombia in Anderson (1999).

***Heteromys australis* (59): COLOMBIA** (17): Nariño: Barbacoas, AMNH 34178–34180, 34182, 34184–34185; Buenavista, 1200 ft [366 m], AMNH 34181, 34183, 34186–34188; Municipio Barbacoas, Corregimiento Altaquer, circa 7 km NNE Altaquer, Reserva Natural del Río Ñambí (FELCA), 1300 m, ICN 13659; Junín, Planada de Maindés, 870 m, UV 3067–3069, 3040A. Valle del Cauca: Las Lomitas, 5000 ft [1524 m], AMNH 32240 (holotype of *Heteromys lomitensis*). **ECUADOR** (27): Carchi: Parroquia Tobar Donoso, El Pailón, 1400 m, EPN 87.1810, 87.1811; Parroquia Tobar Donoso, El Pailón, junto al río Pailón, 1400 m, EPN 87.1746; Parroquia Tobar Donoso, El Pailón, Loma del Tigre, márgen izquierda río Pailón, 1400 m, EPN 87.1786, 87.1787. Esmeraldas: Cantón San Lorenzo, Mataje, EPN 91.3174; Bulim [= Pulún], 160 ft [49 m], FMNH 18871; USNM 172940; San Javier [= San Javier de Cachaví], 60–120 ft [18–37 m], USNM 113304–13307; Alto Tambo, vía Ibarra-Lita-San Lorenzo, Reserva Ecológica Cotacachi-Cayapas, QCAZ 840; Playa de Oro [= Luis Vargas Torres], Estero Zapote, MECN uncataloged, ear tag J. Cevallos 688; Alto Tambo, 2 km S of, 700 m, ROM 105784; Reserva La Mayronga, 80 m, MECN 1611, 1630, 1645; Reserva La Mayronga, Lagarto, 100 m, QCAZ 932–933; Luis Vargas Torres, 2 km S de, EPN 84.561, 84.579; Luis Vargas Torres, 4 km S de, EPN 84.581; Alto Tambo, Hacienda La Granada, Lita, 3 km de, vía a San Lorenzo, 670 m, EPN 84.198, 84.199. Imbabura: Cotocachi, Manduriacu, Los Cedros, 1400–1450 m, EPN 93.3971. Pichincha: Cooperativa Salcedo Lindo, road from Pedro Vicente Maldonado to campamento de CODESA, 4 km S of CODESA camp, UWZM S.31291. **PANAMÁ** (15): Darién: Cana, 1800–2000 ft [549–610 m], USNM 178621, 178698, 178699 (holotype of *Heteromys australis consicus*), 178700, 179595; Amagal, 1000–2000 ft [305–610 m], ANSP 19491–19498, 19499 (holotype of *Heteromys australis pacificus*), 19779. Plus see Anderson (1999) for 134 additional specimens of *H. australis* from Colombia, Panamá, and Venezuela. Note that Alberico et al. (2000) miscited Anderson (1999) by falsely mentioning the documented presence of *H. australis* from the Departamento del Cauca in southwestern Colombia, while failing to note verified specimens from the departments of Antioquia, Boyacá, Caldas, Córdoba, Cundinamarca, Huila, and Quindío or to give credit to reported specimens of this species in the Museo La Salle (MLS, Bogotá) and MCZ collections.

***Heteromys desmarestianus* (species complex; 64): COSTA RICA** (11): Cartago: Angostura, USNM 12903/38590, 12904/38591 (holotype of *Heteromys desmarestianus subaffinis*), 12905/36848; San José: Escazú, 3000 ft [914 m], AMNH 131729 (holotype of *Heteromys desmarestianus underwoodi*); Escazú, Los Higuerones, AMNH 137299–137302; San Gerónimo Pirris, USNM 250348 (holotype of *Heteromys desmarestianus planifrons*), 250349, 256445. **MÉXICO** (10): Chiapas: Chicharras, USNM 77516 (holotype of *Heteromys goldmani*), 77577, 77579–77582, 77694; Veracruz: Motzorongo, USNM 63718, 63719 (holotype of *Heteromys temporalis*), 63720. **PANAMÁ** (43) Colón: Río Indio, near Gatún, USNM 170919–170920, 170975, 170976 (holotype of *Heteromys zonalis*); Chiriquí: Boquete, 4000–5800 ft [1219–1768 m], MCZ B10355, B10356 (holotype of *Heteromys repens*), B10358, B10360–B10361; Cerro Pando, ANSP 17835 (holotype of *Heteromys desmarestianus chiriquensis*), 17836–17837, 18374–18377; Darién: Mount Pirri, near head of Río Limón, 4500–5200 ft [1372–1585 m], USNM 178998–179004, 179006–179015, 179016 (holotype of *Heteromys crassirostris*), 179018–179020; Panamá: Cerro Azul, 2500–3000 ft [762–914 m], USNM 171107 (holotype of *Heteromys panamensis*), 171108–171111, 171128.

***Heteromys gaumeri* (2): MÉXICO** (2): Campeche: 7 km N, 51 km E Escarcega, KU 93644; 103 km SE Escarcega, KU 93647.

***Heteromys nelsoni* (2): MÉXICO** (2): Chia-

PAS: Pinabete, USNM 77920 (holotype of *Heteromys nelsoni*), 77578.

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

Heteromys teleus **(31): ECUADOR** (31): COTOPAXI: San Francisco de las Pampas, Reserva Bosque Nublado Otonga [= Bosque Integral Otonga], 1900–2000 m, QCAZ 1788. ESMERALDAS: Quinindé, EPN .22 (provisional identification based on study skin). GUAYAS: Cerro Manglar Alto, eastern slope, Camp I, 1200 ft [366 m] (camp), [specimens from 1400 feet, = 427 m; G.H.H. Tate field notes, May 1923], AMNH 64675–64679; Cerro Manglar Alto, western slope, Camp II, 1500 ft [457 m] (camp), [specimens from 2000 feet, = 610 m; G.H.H. Tate field notes, May 1923], AMNH 64680–64696. LOS RÍOS: Río Palenque Biological Station [= Río Palenque Science Center], 220 m, KU 149132–149135; Río Palenque Science Center, Santo Domingo, 47 km S of (by road), USNM 528573; Cantón Vinces, Parroquia Palenque, Jauneche, Estación Biológica Pedro Franco Dávila, 50 m, EPN 91.3038. PICHINCHA: La Concordia, 2 km de, Bosque Protector La Perla, 220 m, QCAZ 905 (provisional identification based on study skin).

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