

A new species of *Habromys* (Muroidea: Neotominae) from México, with generic review of species definitions and remarks on diversity patterns among Mesoamerican small mammals restricted to humid montane forests

Michael D. Carleton, Oscar Sánchez, and Guillermina Urbano Vidales

(MDC) Department of Systematic Biology, Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0108, U.S.A.; (OS), Avenida Ixtlahuaca 609, Col. Sánchez, Toluca 50040, Estado de México, México; (GUV), Departamento de Zoología, Instituto de Biología, UNAM Circuito exterior s/n, Ciudad Universitaria, Coyoacán, A.P. 70-153, D.F., México 04510

Abstract.—A new species of *Habromys*, *H. delicatulus*, is described from an isolated patch of cloud forest situated on a northern exposure of the Cordillera Neovolcanica, Estado de México. The species is the smallest so far known in the genus and is further characterized by its delicate cranial features. Morphometric comparisons with the five other species-group taxa currently allocated to the genus recommend the elevation of *ixtlani* Goodwin, 1964, as a species distinct from *Habromys lepturus* (Merriam, 1898). *Habromys lophurus* (Merriam, 1908), known from highlands east of the Isthmus of Tehuantepec, appears to be the sister taxon to the former pair, each restricted to separate Oaxacan ranges west of the Isthmus. *Habromys chinanteco* (Robertson & Musser, 1976) is retained as a species, but its possible status as a junior synonym under *H. simulatus* (Osgood, 1904) warrants continued investigation with improved samples. The montane distribution of *Habromys* in naturally discontinuous humid-forest associations of northern Mesoamerica is considered in the context of diversity patterns summarized for other small terrestrial mammals confined to such forests.

Resumen.—Se describe una nueva especie de *Habromys*, *H. delicatulus*, de un manchón aislado de bosque mesófilo de montaña situado en una ladera de la Cordillera Neovolcánica expuesta al norte, en el Estado de México. La especie se caracteriza por sus rasgos craneanos delicados y por su tamaño pequeño, el más pequeño conocido hasta ahora para el género. Comparaciones morfométricas de los otros cinco taxa (grupos de especies) actualmente incluidos en el género, recomiendan la elevación de *Peromyscus ixtlani* Goodwin, 1964, al estado de especie distinta de *Habromys lepturus* (Merriam, 1898). *Habromys lophurus* (Merriam, 1908) conocido de tierras altas al este del Istmo de Tehuantepec, parece ser taxón hermano del par antes mencionado, cada uno de cuyos miembros está restringido a sierras Oaxaqueñas separadas, ambas al oeste del Istmo. *Habromys chinanteco* (Robertson y Musser, 1976) se retiene como especie, pero su posible estado como sinónimo menor bajo *H. simulatus* (Osgood, 1904) amerita continuar la investigación con mejores muestras. Se pondera la distribución montañesa de *Habromys* en asociaciones naturalmente discontinuas de bosque húmedo del norte de Mesoamérica, en el contexto de los patrones de diversidad resumidos para otros mamíferos terrestres pequeños confinados a esos bosques.

In April and May 1985, an exploratory survey of small mammals in the northern part of the State of Mexico uncovered several kinds of rodents that inhabited montane forest near the town of Jilotepec. Among the species samples collected in a cool, moist ravine were several specimens of a small-bodied mouse with a relatively short, hairy tail and large pinnae. Subsequent museum study has convinced us that this distinctive species represents an unnamed form of the genus *Habromys* (sensu Carleton 1989) that we name and describe herein. The necessity of performing critical comparisons to other *Habromys* afforded us the opportunity to systematically review the genus and to amplify the geographic distribution of named forms based on unreported material. Finally, the humid forest, montane habitus of the genus encouraged comparison of distributional patterns among other species of small terrestrial mammals in Mesoamerica.

Materials and Methods

Specimens reported herein consist principally of skins with their associated skulls and are contained in the following museums and institutions: American Museum of Natural History, New York City (AMNH); Monte L. Bean Life Science Museum, Brigham Young University, Provo (BYU); Field Museum of Natural History, Chicago (FMNH); Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México, México City (CNMA); Museum of Natural History, University of Kansas, Lawrence (KU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Zoology, University of Michigan, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Nineteen craniodental variables were measured to 0.01 mm, using hand-held digital calipers while viewing crania under a stereomicroscope. These measurements,

and their abbreviations as used in text and tables, include: occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of braincase (BBC); height of braincase (HBC); breadth across the occipital condyles (BOC); least interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); postpalatal length (PPL); length of the bony palate (LBP); length of the upper diastema (LD); length of left incisive foramen (LIF); breadth of the incisive foramina (BIF); breadth of palate between the first molars (BM1s); width of mesopterygoid fossa (WMF); breadth of the zygomatic plate (BZP); coronal length of the maxillary toothrow (CLM); width of the first upper molar (WM1); and breadth across the upper incisor tips (BIT). In addition, standard external dimensions and body mass (weight in grams) were transcribed from skin tags as given by the collector: total length (TOTL), tail length (TL), hindfoot length (HFL), and ear length (EL).

Except for the large series of *H. lepturus ixtlani* collected from the slopes of Cerro Pelón, northern Oaxaca, most locality samples of *Habromys* in collections are small, typically numbering from 3 to 10 specimens. For analytical purposes, 13 operational taxonomic units (OTUs), several composed of specimens from nearby localities, were recognized, listed below according to current species taxonomy. Full provenience and catalog numbers are provided in the Taxonomic Summary.

Habromys chinanteco: OTU 1—México, Oaxaca, NE slopes Cerro Pelón, Vista Hermosa and vicinity (n = 6).

H. lepturus ixtlani: OTU 2—México, Oaxaca, NE slopes Cerro Pelón, Vista Hermosa and vicinity (n = 51); OTU 3—México, Oaxaca, Cerro Machín (n = 26); OTU 4—México, Oaxaca, SW slopes Cerro Pelón, Llano de las Flores and vicinity (n = 68).

H. l. lepturus: OTU 5—México, Oaxaca, upper slopes of Cerro Zempoaltepec (n = 35).

H., new species: OTU 6—México, Mexico, near Jilotepec ($n = 7$).

H. lophurus: OTU 7—México, Chiapas, Pinabete and Triunfo ($n = 11$); OTU 8—México, Chiapas, San Cristobal and Cerro Tzontehuiz ($n = 5$); OTU 9—Guatemala, Huehuetenango, near San Juan Ixcoy and Todos Santos ($n = 14$); OTU 10—Guatemala, Huehuetenango, Santa Eulalia ($n = 15$); OTU 11—El Salvador, Chalatenango, Los Esesmiles ($n = 4$).

H. simulatus: OTU 12—México, Sierra Madre Oriental, sites in Hidalgo and Veracruz ($n = 4$); OTU 13—México, Oaxaca, near Puerto de la Soledad ($n = 3$).

Standard descriptive statistics (mean, range, standard deviation, coefficient of variation) were derived for the OTUs. One- and two-way analyses of variance, discriminant functions, and principal component analyses were computed using the 19 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and loadings are expressed as Pearson product-moment correlation coefficients of the components with the original cranial variables. Means and ranges of external variables are provided as a guidance in identification (see Appendix 1) but were not considered in multivariate analyses. All analytic procedures were conducted using Systat (Version 9.01, 1998), a series of statistical routines developed for microcomputers.

The occurrence of small terrestrial mammals restricted to montane forest associations was summarized for seven Mesoamerican mountainous regions (Table 6), whose names as employed in the text and geographic limits are understood as follows: (1) Cordillera Neovolcanica; (2) Sierra Madre Oriental; (3) Oaxacan Highlands—principally the Sierras de Juarez, Zempoaltepec, Aloapaneca, Cuatro Venados, Yucuyacua in northcentral Oaxaca; (4) Sierra Madre del Sur-West—the highland block in central Guerrero, mostly localities in the Sierra de Atoyac; (5) Sierra Madre del

Sur-East—coastal ranges in southern Oaxaca, principally the Sierra de Miahuatlán; (6) Nuclear Central America sensu Savage (1982) and others—highlands of northern Central America between the Isthmus of Tehuantepec and Nicaraguan Depression; and (7) Talamancan Highlands—the highland block in southern Central America, principally the Cordilleras Tilarán, Central, and de Talamanca of Costa Rica, and Chiriqui of western Panama. Humid montane forest is broadly used herein, referring to cloud forest (Rzedowski 1986) of middle elevations as well as pine-oak and pine-oak-fir associations of middle to upper elevations (also see, Hernández-Baños et al. 1995). These forest communities embrace the Subtropical Rainforest and Wet Forest, Lower Montane Wet and Moist Forest, and Montane Wet and Moist Forest zones of Holdridge (1967).

Faunal similarities among the seven mountain regions were assessed by means of the Jaccard Index and parsimony analysis of endemism. The Jaccard Index is a matching coefficient for binary data that scales similarity to range from 0 to 1:

$$\text{Jaccard Index} = \frac{N_C}{N_1 + N_2 - N_C},$$

where N_1 = the number of species present at site 1, N_2 = the number of species at site 2, and N_C = the number of species common to both sites (Hayek, 1994). The indices from the pairwise comparisons were clustered using a nearest-neighbor routine as implemented by Systat. Parsimony analysis of endemism (PAE, Rosen & Smith 1988) associates pre-defined geographic areas according to their shared taxa by the criterion of maximum parsimony, by analogy treating areas as taxa and species occurrence (absence-presence, 0–1) as characters (Table 6). We used PAUP*, version 4.0b8 (Swofford 2001), to find area-relationship trees of minimal length, using the branch-and-bound option and the accelerated transformation routine to optimize intermediate character state transformations. Characters

were unweighted, and trees were rooted using a hypothetical outgroup devoid of all species.

Habromys delicatulus, new species

Figs. 1–3, 12; Appendix 1

Holotype.—CNMA 22439, an adult male prepared as skin, skull, partial skeleton (tibiae, fibulae, and right femur missing), and phallus in fluid; collected 15 April 1985 by Oscar Sánchez (original number OSH 580).

The general condition of both skin and skull is good. However, the extreme tip of the tail is loosely attached, and the thin arch of pterygoid bone that forms the ventral rim of the left foramen ovale accessorius, at the posterolateral corner of the parapterygoid fossa, is missing.

External measurements recorded (in mm) on the skin tag include total length, 159; tail length, 80; hindfoot length, 19; and ear length, 18.5. The weight is given as 12.5 grams. The animal was noted as having scrotal testes, measuring 6×4 mm in size.

Type locality.—México, Estado México, Municipio Jilotepec, Dexcaní Alto, 2 km E and 3.5 km S Jilotepec, Cañada de la Ermita, 2570 m (19°56'N, 99°30'W).

Diagnosis.—A species of *Habromys* characterized by tiny size (total length = 150–165 mm; occipitonasal length = 22–24 mm; maxillary toothrow = 3.2–3.5 mm); cranium gracile in appearance with short, slender rostrum, thin zygomatic arches, and narrow zygomatic plate; interparietal comparatively narrow, its lateral apices separated from squamosal by a broad gap; tail approximately as long as length of head and body; pinna relatively long and wide, auditory bulla (ectotympanic) relatively expanded.

Referred specimens.—Six, all collected from the type locality: CNMA 22437, subadult male, skin and skeleton, collected 22 May 1985 by Juan Galván S. (JGS); CNMA 22438, young female, skin and skeleton, collected 22 May 1985 by JGS;

CNMA 22440, female, skin and skeleton, collected 22 May 1985 by Oscar Sánchez (OSH); CNMA 22441, male, skin and skeleton, and stained baculum, collected 17 April 1985 by OSH; CNMA 22442, male, skin and skeleton, collected 22 May 1985 by OSH; CNMA 25908, male, skin, skull, and body in alcohol, collected 6 September 1986 by OSH.

Description.—Small size evident in all quantified dimensions of the skin and skull (Appendix 1). General effect of the upperparts medium to rich brown, not appreciably darker over the middle dorsum as in some *Habromys*. Fur soft, fine, and dense, the cover hairs averaging about 5–6 mm long and the fine guard hairs 8–10 mm long over the midrump. Individual cover hairs shiny lead gray over their basal three-quarters, tipped with a short band of bright buff and usually an extremely short dark terminal band. Buffy band more intense along the sides, approaching ochraceous and suggesting a more or less well defined lateral line in some specimens, particularly along the hindquarters. Area of brownish black extending from side of rostrum to and around the eye as an indistinct eye ring. Tops of forefeet white to the carpus. Underparts appear bright gray or grayish-white, an impression formed by the lustrous white tips of the ventral cover hairs incompletely obscuring their plumbeous bases. Hairs of the chin and throat typically white to the base.

The longest mystacial vibrissae measure 30–35 mm and extend appreciably beyond the dorsal rim of the pinnae when appressed to the side of the head.

Pinnae proportionally large and prominent, about as long as the hindfoot (Fig. 1). Externally, darkly pigmented and covered by short, dusky brown hairs that become denser towards the anterior and dorsal rim; internally, more lightly pigmented and less heavily furred, nearly naked and flesh-colored at the concha. As a general impression, pinna coloration blends with that of the dorsum.

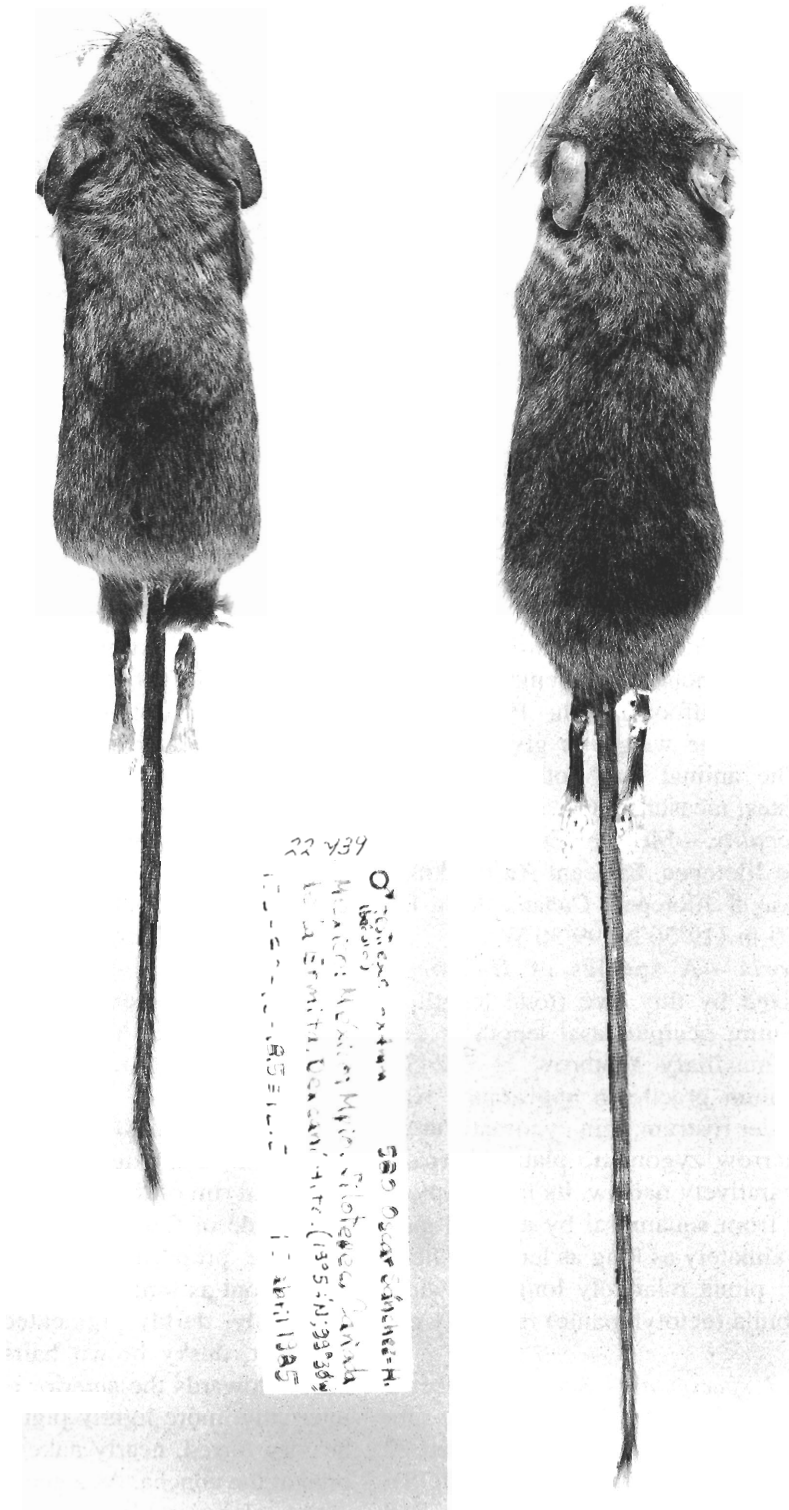


Fig. 1. Dorsal view (about natural size) of the study skins of small *Habromys*. Left, *H. delicatulus*, new species (CNMA 22439, holotype), an adult male from Cañada de la Ermita, México; right, *H. chinanteco* (AMNH 254780), an adult female from 16 mi SSW La Esperanza, Oaxaca.

Length of tail vertebrae more or less equal to the head and body. Caudal hairs moderately long, obscuring scalar pattern except near the base; hairs becoming more elongate and weakly penicillate toward the tip; tail bicolouration moderately defined, dark brown above and white below, though dorsal-ventral contrast not sharply delimited as in *Peromyscus maniculatus*.

Hindfoot relatively short and moderately wide, with digit V nearly as long as digits II–IV. Plantar pads six in number, relatively large and fleshy, the interdigital pads clustered together toward the base of the digits. Dark fur of the lower limb continues across the tarsus and onto the middorsal metatarsus as a dusky streak; distal metatarsus and tops of digits clothed with silvery white hairs that terminate as a tuft or spray of hairs arching over the claws and beyond their tips. White hairs thinly cover the heel up to the thenar pad; remainder of plantar surface naked.

Construction of cranium delicate, suggesting a miniaturized version of *H. simulatus* (Figs. 2, 3). Rostrum comparatively short for the genus (LR about 32% of ONL), narrow and attenuate toward the nasal tips; tips of nasals slightly upturned; nasolacrimal capsules not appreciably flared. Interorbital region hourglass-shaped (amphoral) as viewed dorsally, devoid of supraorbital ridges or projecting shelves. Zygoma extremely slender, particularly across the jugal bones, and slightly convergent anteriorly as viewed from above. Zygomatic notch barely evident, no formation of anteriorly projecting spine; leading margin of zygomatic plate straight and nearly vertical. Braincase globoid, smoothly rounded and unmarked by temporal and lambdoidal ridging. Interparietal relatively short and narrow, its lateral edges separated from the squamosal by broad contact of the exoccipital and frontal. Dorsal profile of skull moderately vaulted, nearly straight over the facial region and more conspicuously arched over the calvarium.

Incisive foramina relatively long (LIF

about 80% of LD), slightly narrower and convergent anteriorly but wider and parallel-sided posteriorly, their rear border projecting between the anterior root of the M1s and reaching to the level of the anterocone. Bony palate nearly flat, pierced by a pair of small posterior palatine foramina, which are round to oval and open within the maxillopalatine suture where M1 and M2 abut. Forward margin of mesopterygoid fossa terminates more or less even with the rear edge of the M3s; shape of anterior portion horseshoe-like, slightly convergent in the posterior region; roof of mesopterygoid fossa incomplete, interrupted with spacious sphenopalatine vacuities. Parapterygoid fossae typically with large medial fenestra. Middle lacerate foramen slitlike, separated from the postglenoid foramen by stout overlap of the tegmen tympani and posteroventral tab of the squamosal. Postglenoid and subsquamosal foramina medium-sized, approximately equal in area and together delineating a slender hamular process. Carotid circulatory pattern complete (stapedial and sphenofrontal foramina present, posterior opening of the alisphenoid canal large, shallow groove crosses the inner surface of the squamosal and alisphenoid bones). Alisphenoid struts present on both sides of all individuals composing the type series. Ectotympanic bullae relatively inflated, nearly the size of those possessed by the larger-bodied *H. simulatus*; large fenestra perforates the posterodorsal surface of the mastoid bullae.

Coronoid process of mandible short, somewhat blunt, and not rising above level of condyloid process; sigmoid notch correspondingly shallow, noticeably less well defined than concavity of the angular notch. Lateral surface of ascending ramus smooth, without formation of capsular process of incisor; inferior and superior masseteric ridges poorly defined, their anterior union occurring below the middle of m1.

Upper incisors weakly opisthodont to nearly orthodont; enamel faces of upper and lower incisors colored pale yellow. Molar

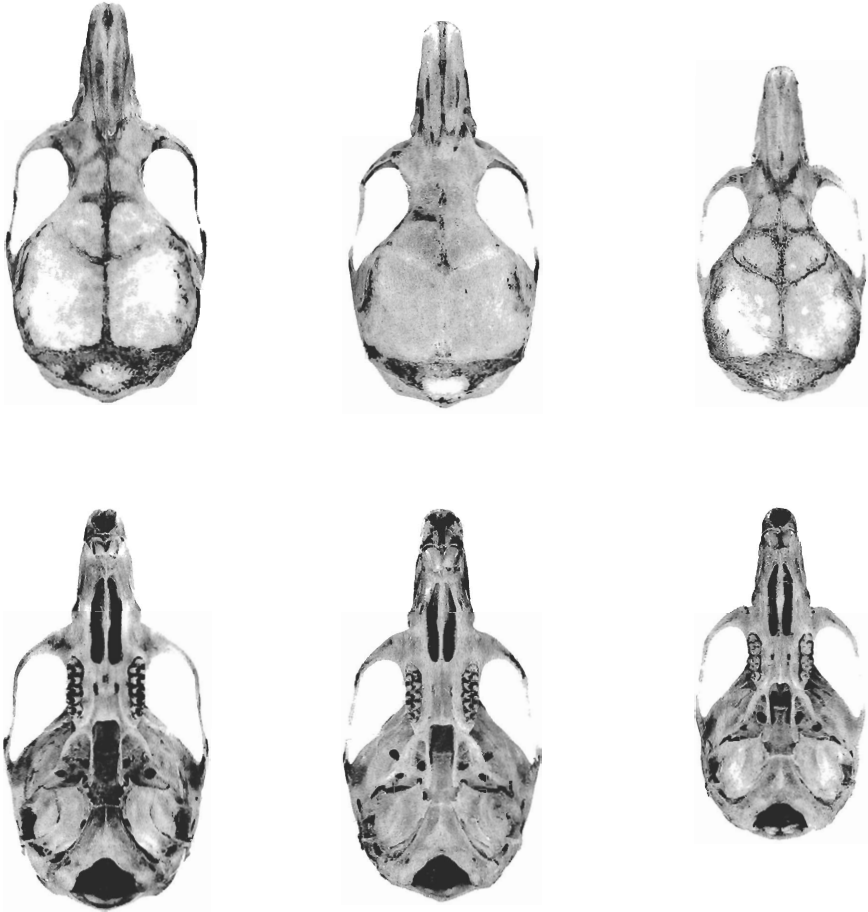


Fig. 2. Dorsal and ventral views (about 2 \times) of adult crania illustrating the three smaller forms of *Habromys*. Left pair, *H. simulatus* (BYU 15052), a male from 1.5 mi S Puerto del la Soledad, Oaxaca; middle pair, *H. chinanteco* (AMNH 254780), a female from 16 mi SSW La Esperanza, Oaxaca; and right pair, *H. delicatulus*, new species (CNMA 22439, holotype), a male from Cañada de la Ermita, México.

rows parallel to one another. Upper first and second molars with complete mesolophs but lacking ectolophs; mesolophids of lowers incomplete or absent. M1 ovate with anterocone narrower than width across protocone-paracone and apparently lacking anteromedian sulcus; M3 circular in outline and small, about half the occlusal area of M2. Anteroconid of m1 weakly bifurcate; m3 about two-thirds as large as m2, apparently retaining a short posteroflexid (second primary fold) in unworn teeth.

Dorsal vertebrae consist of thirteen thoracics and six lumbar; first rib articulates with the transverse process of both the sev-

enth cervical and first thoracic vertebra; entepicondylar foramen present (skeletal traits based on specimens CNMA 22439 and 22441).

Glans penis short, narrow, and awl-shaped, widest at the base and gradually tapering toward a blunt tip; urinary meatus opens just below tip; glans surface nonspiny; dorsal and ventral lappets absent (phallic traits based on CNMA 22439 and 25908). Baculum longer than glans penis (in CNMA 22439, bacular length = 4.7 mm, glans length = 2.6 mm, and glans width = 0.5 mm; in CNMA 25908, bacular length = 4.9 mm, glans length = 3.1 mm,

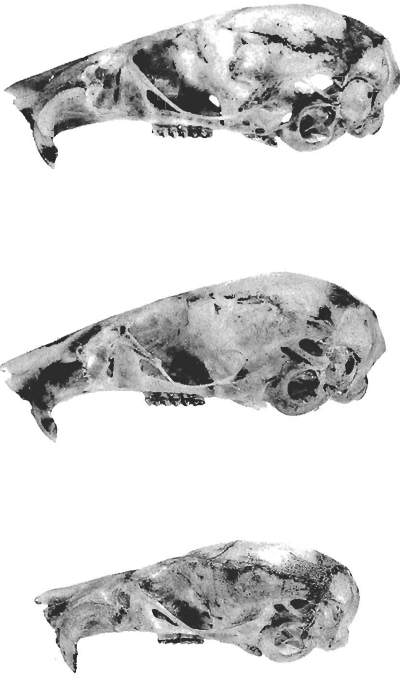


Fig. 3. Lateral view (about 2 \times) of adult crania illustrating the three smaller forms of *Habromys*. Top, *H. simulatus*; middle, *H. chinanteco*; and bottom, *H. delicatulus*, new species (same specimens as in Fig. 2).

and glans width = 0.5 mm); cartilaginous cap unrecognizable on single cleared and stained specimen (CNMA 22441). Vesicular glands extremely small, bulbourethral glands relatively large (based on CNMA 25908). Stomach apparently discoglandular based on single poorly preserved specimen (CNMA 25908).

Comparisons.—The recognition of *H. delicatulus* is at once obvious based on its very small size, a contrast which alone permits no confusion in distinguishing the new species from other described forms of *Habromys* (Figs. 2, 9; Appendix 1). Morphometric analyses of craniodental measurements reinforce the impression of its delicately constructed skull and diminutive size compared with those of other species. The uniformly large and positive correlations between nearly all variables and the first principal component (Table 1) emphasize the predominant influence of size on this

Table 1.—Results of discriminant function analysis performed on intact specimens (N = 209) representing 13 OTUs of *Habromys* (see Fig. 4).

Variable	Correlations	
	CV 1	CV 2
ONL	0.95	-0.06
ZB	0.91	0.11
BZP	0.88	0.12
IOB	0.73	-0.30
BBC	0.81	-0.16
BOC	0.90	0.03
HBC	0.72	0.15
LR	0.93	-0.19
BR	0.82	-0.08
LD	0.90	-0.23
LIF	0.88	0.11
BIF	0.78	0.05
LBP	0.88	-0.22
BM1s	0.67	-0.25
WMF	0.67	0.17
PPL	0.92	-0.09
CLM	0.94	0.28
WM1	0.96	0.12
BIT	0.82	0.08
Canonical correlations	0.98	0.90
Eigenvalues	24.6	4.5
% Variance	76.2	13.8

factor and account for the pronounced phenetic isolation of the sample of *H. delicatulus* (Fig. 4). Size, too, undoubtedly explains its closer linkage to the other small *Habromys* (i.e., *H. chinanteco* and *H. simulatus*) in UPGMA amalgamation of group centroids based on Mahalanobis distances (Fig. 4). Whether this phenetic association also reflects phylogenetic affinity invites future investigation that integrates other kinds of systematic information.

In addition to its small size and correspondingly fine definition of its features, *H. delicatulus* displays certain proportional differences that suggest its specific distinction. Foremost among these is the comparatively large size of the pinnae and auditory (ectotympanic) bullae. The length of ear from notch measured on specimens of *H. delicatulus* generally exceeds values recorded for those of *H. chinanteco* and *H. simulatus*, with minimal overlap (Appendix 1); absolute size of pinnae in *H. delicatulus*

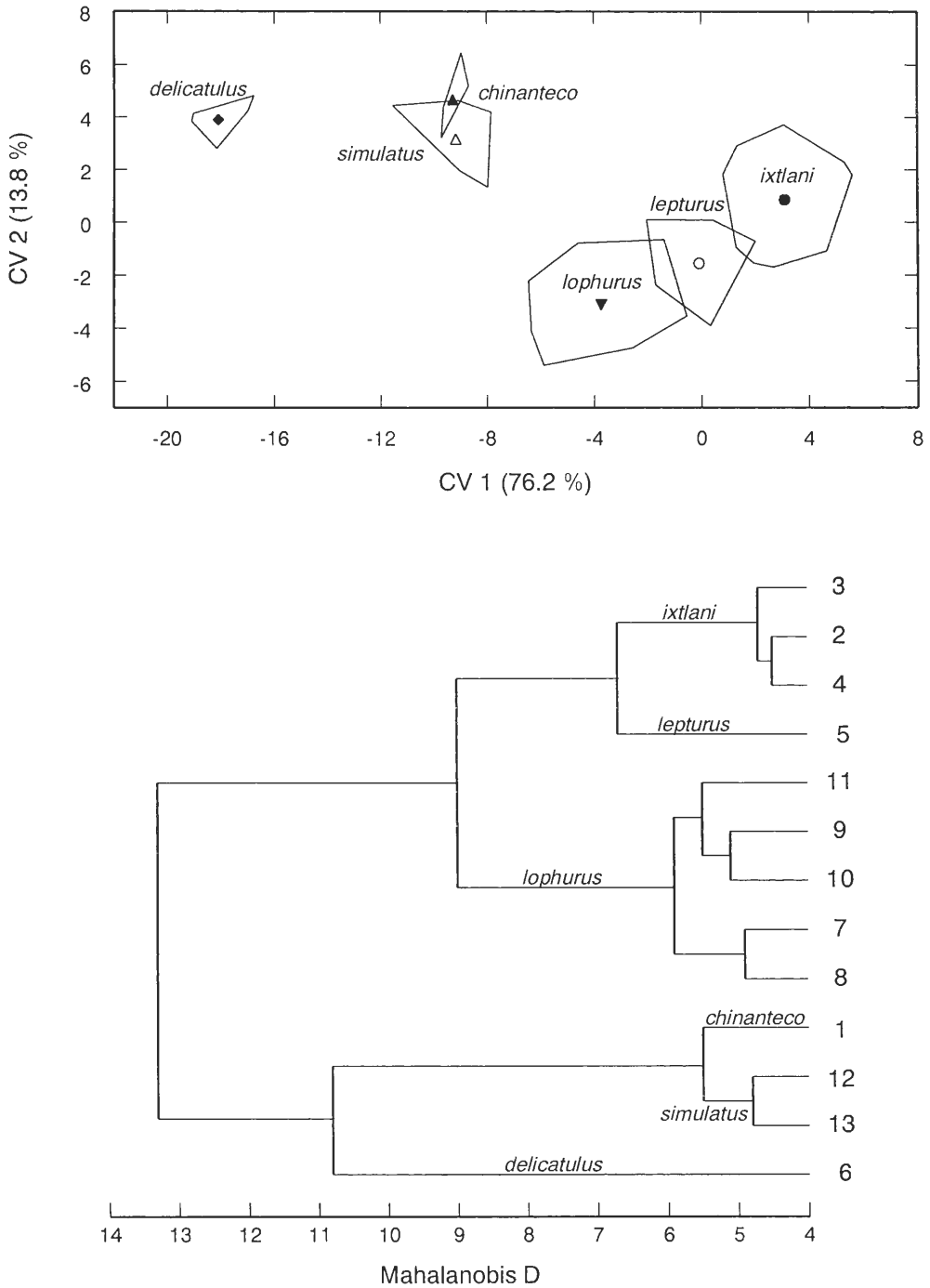


Fig. 4. Results of discriminant function analysis performed on 19 log-transformed craniodental variables as measured on 203 intact specimens representing all 12 OTUs of *Habromys*. Top, projection of specimen scores on first two canonical variates extracted (maximal dispersion for the large samples of *ixtlani*, *lepturus*, and *lophurus* are represented by a polygon around the bivariate centroid); bottom, UPGMA phenogram based on Mahalanobis distances between the 12 OTU centroids. See Table 1.

most closely approximates the much larger *H. lophurus*. Although we, regrettably, did not quantify size of auditory bullae, the relatively greater inflation of the bullae in *H. delicatulus* is visually apparent in side-by-side comparisons of crania (Fig. 2). The tail in examples of *H. delicatulus* appears to be the shortest in the genus, only subequal to head-and-body length (Appendix 1); in most other forms of *Habromys*, the tail exceeds the length of head and body (TL about 105–110% of HBL). Also noteworthy are the relatively short, attenuate rostrum and broad interorbital region that characterize the series of *H. delicatulus*.

Although the smallest species of *Habromys*, *H. delicatulus* possesses most diagnostic traits identified for the genus (e.g., as emended by Carleton 1989). Its hindfoot is short and relatively broad, with an elongate fifth digit; the plantar surface of the heel is thinly haired; and the zygomatic plate is narrow with little forward extension or elaboration of a dorsal notch. Attributes of the reproductive tract in *H. delicatulus*, insofar as verifiable (see below), conform to the key traits central to the definition of *Habromys* (Hooper 1958, Hooper & Musser 1964, Linzey & Layne 1969). Other resemblances, presumably plesiomorphic, shared by *H. delicatulus* and other *Habromys* taxa include the amphoral interorbital configuration unmarked by supraorbital ridging, the round and smooth braincase, and relatively complex molars (mesolophids present, retention of posteroflexid on m3). Furthermore, the well-furred tail in *H. delicatulus* and its modest expression of penicillation are comparable to other species of *Habromys*.

Ecological notes.—The type locality is situated within the northernmost escarpments of the Cordillera Neovolcanica (Fig. 12). Huge boulders are a conspicuous feature of the landscape and shape the mouth of the steep ravine where individuals of *Habromys delicatulus* were captured. Such rocks are considerably intemperized, but their size and disposition provide seclusion

and consequently maintain a moister micro-environment in comparison with adjacent areas. The general area is covered by thick forests of oak (*Quercus* spp.) intermingled with small, localized patches of oyamel (*Abies* sp.).

The habitat in the ravine sheltering *H. delicatulus*, however, can be characterized as a relict of montane cloud forest, with indicative tree species such as *Ilex toluhana*, *Garrya* aff. *laurifolia*, and *Cornus* aff. *disciflora*. Oaks, madroños (*Arbutus* sp.), and tepozanes (*Buddleja americana*) are also present, as well as succulent orchids growing on the branches of trees. In addition, the understory is thick and dominated by *Phytolacca* sp., at least during the rainy season. In this region, such montane cloud forest patches are commonly located on northwardly facing slopes, an orientation that describes the Jilotepec site. This physiographic aspect, as well as the steepness and height of the sheltering rock walls, promotes a fairly uniform microclimate, and a small spring at the bottom contributes to the maintenance of these conditions throughout the year. Contrast in ambient humidity over short distances is striking, for on top of the exposed rock walls outside the ravine, some xerophytic vegetation is present, such as globular Cactaceae, century plants, and Gramineae. Pockets of fog-enshrouded forest, as found in the Cañada de la Ermita, are common (or once were so) in the eastern portion of the Cordillera Neovolcanica, and have formed a biogeographic microcosm where other vertebrates more narrowly restricted to cloud forest, such as certain plethodontid salamanders, have undergone localized radiations (Wake & Lynch 1976, Darda 1994).

Habromys delicatulus appears to be rather if not mainly arboreal in habits. Six of the seven specimens were obtained by traps set in trees as described by Sánchez (1996). Five were obtained in *Ilex toluhana* trees, at heights above ground of 4.3 m (CNMA 22440), 3.2 m (CNMA 22439, holotype), 2.7 m (CNMA 22442), 1.3 m (CNMA

25908), and 0.9 m (CNMA 22438); another was collected in a *Quercus* sp. at 2.1 m (CNMA 22441). Although many traps were placed in terrestrial locations, where other species of rodents were captured, only one example (CNMA 22437) of *H. delicatulus* was obtained on the forest floor.

At the time of the survey, certain rodent species were comparatively abundant at the type locality (*Peromyscus levipes*, *P. difficilis*, *Liomys irroratus*), while others occurred in lesser numbers (*Habromys delicatulus*, *Reithrodontomys fulvescens*, *Neotoma mexicana*). The easternmost record of *Nelsonia goldmani*, a species endemic to the Cordillera Neovolcanica, has been reported at a nearby site within the Cañada de la Ermita (Engstrom et al. 1992), an outlying occurrence which also emphasizes the relictual nature of this montane forest patch.

Etymology.—The specific epithet *delicatulus* acknowledges the new species' slightly built cranium and overall diminutive size.

Morphological Differentiation Among Other Forms And Taxonomic Recommendations

Aside from supporting recognition of a new species, *H. delicatulus*, the amount of morphometric divergence uncovered among other named taxa is equally informative taxonomically, in particular that revealed between the smaller forms *H. simulatus* and *H. chinanteco* and that between the larger *H. lepturus* and its present synonym *ixtlani* Goodwin (1964). First, we focus separately on these two issues, drawing upon examples of the intermediately sized species *H. lophurus* as a yardstick of intraspecific variation for the morphometric comparisons implemented. Second, we review qualitative traits of the reproductive tract and postcranial skeleton exhibited by the smaller species and their bearing on the definition of the genus.

Sexes were combined in all multivariate analyses, a procedural necessity warranted

by the inadequate sample sizes of the smaller *Habromys* and *H. lophurus*. Secondary sexual dimorphism in cranial size is, in fact, unremarkable in the two largest samples available, those of *H. lepturus ixtlani* (OTUs 2, 4). Contribution of sex to significant within-sample variation was recorded for only one variable (CLM) among the two OTUs (Table 2), a rarity (one of 38 two-way ANOVAs implemented = 2.6%) plausibly explained as a Type I sampling error. In contrast, significant age-related variation in size, probably due to postweaning growth, is commonplace in both samples, characterizing about half of the skull dimensions measured. Furthermore, the pattern of pronounced age-related differences in these two OTUs is comparable in terms of the variables involved—notably the largest measurements (ONL, ZB, PPL) and those measured on the facial region (LR, BR, LD, LIF)—and the magnitude of the F ratios (Table 2). Such patterns of nongeographic variation according to age and sex factors generally conform to those reported for other species of neotropical muroids (e.g., Ramírez-Pulido et al. 1991, Carleton & Musser 1995, Martínez Coronel et al. 1997), and while sample age variation can be substantial, it emerges as inconsequential relative to the morphometric divergence of closely related (congeneric) taxa (e.g., Carleton & Musser 1989, 1995; Voss & Marcus 1992; Carleton et al. 1999).

Habromys simulatus and *H. chinanteco*.—Since Osgood (1904) described it as a species of *Peromyscus*, *simulatus* has remained a well defined but obscurely known form. It was long represented by only the two specimens from the type locality (Jico, Veracruz) until a third was uncovered by Robertson & Musser (1976) from near Zacualpan, Veracruz. The additional localities reported here (see Taxonomic Summary), collected by BYU field crews in Hidalgo and northwesternmost Oaxaca, suggest that the species is distributed more widely along middle to upper eastern slopes of the Sierra Madre Oriental (Fig. 12), probably adhering

Table 2.—Significance levels and F values derived from two-way analyses of variance of 19 cranial dimensions as measured for sex and age cohorts in two large OTUs of *Habromys lepturus ixtlani*.

	OTU 2			OTU 4		
	Age	Sex	Interaction	Age	Sex	Interaction
ONL	15.7***	0.7	0.3	14.2***	1.8	0.2
ZB	15.3***	1.5	0.3	7.0**	0.3	0.2
BZP	2.2	0.3	1.1	1.6	0.7	1.0
IOB	0.2	0.4	0.4	0.4	0.3	1.5
BBC	0.9	0.1	1.2	0.3	3.1	0.2
BOC	1.0	3.6	0.4	0.8	0.4	3.4*
HBC	0.3	1.5	2.7	0.9	0.0	0.3
LR	12.7***	0.9	0.4	8.1**	1.3	0.5
WR	3.6*	0.8	0.5	7.2**	0.2	1.6
LD	20.1***	2.6	1.2	23.1***	0.1	1.3
LIF	6.4**	1.8	0.0	6.2**	0.2	0.3
BIF	0.1	0.3	1.2	0.4	0.2	0.1
LBP	5.3**	1.5	0.1	3.0	0.8	0.3
BM1s	2.7	3.3	0.5	0.4	0.3	0.1
WMF	8.6**	0.5	0.6	1.3	1.4	0.1
PPL	14.8***	0.0	0.3	8.2**	2.7	0.1
CLM	0.9	0.5	3.0	11.5***	4.0*	1.7
WM1	1.1	1.1	1.2	3.2*	3.6	1.7
BIT	11.3***	0.0	0.1	6.6**	0.4	0.1

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

to the band of cloud forest as documented for certain other small rodents in the region (*Megadontomys nelsoni*, Carleton 1989; *Microtus quasiater*, Ramírez-Pulido et al. 1991; *Oryzomys chapmani*, Musser & Carleton 1993; *Peromyscus aztecus*, Carleton 1979; *P. fuvvus*, Martínez-Coronel et al. 1997).

While Osgood (1909) viewed *simulatus* as a miniature version and close kin of *lophurus*, a closer probable relation was later discovered in mountains of northern Oaxaca and described by Robertson & Musser (1976) as *Peromyscus chinanteco*. These authors viewed the new species as a member of the subgenus *Habromys* “most closely related to *simulatus*” and accordingly confined their differential comparisons to other subgeneric forms as circumscribed by Hooper & Musser (1964) and Hooper (1968).

Morphometric evaluations of our 19 craniodental measurements suggest that *chinanteco* is indeed closely related to, if not conspecific with, Osgood’s *simulatus*.

In principal component analysis, factor scores of *simulatus* and *chinanteco* specimens are interspersed, and together resemble, excepting the fewer specimens available, the elliptical spread of component values derived for examples of *H. lophurus* (Fig. 5). Variable correlations with PC I generally bear out the much larger size of *H. lophurus* with regard to *simulatus*-*chinanteco*; loadings on PC II indicate that the latter pair, however, exhibit a comparatively broader skull (BBC, BR, IOB, BM1s) and daintier teeth (CLM, WM1) than is characteristic of *H. lophurus* (Table 3).

Unlike principal component results, a scatter plot of the first two canonical variates (cumulative proportion of variation = 87%) extracted from eight-group discriminant function analysis divulges close proximity but no overlap of specimen scores representing the sample of *chinanteco* and those of *H. simulatus* (Fig. 6). The largest hiatus disclosed, however, separates OTUs of *H. lophurus* from those of *H. chinanteco* and *H. simulatus* and reflects the decidedly

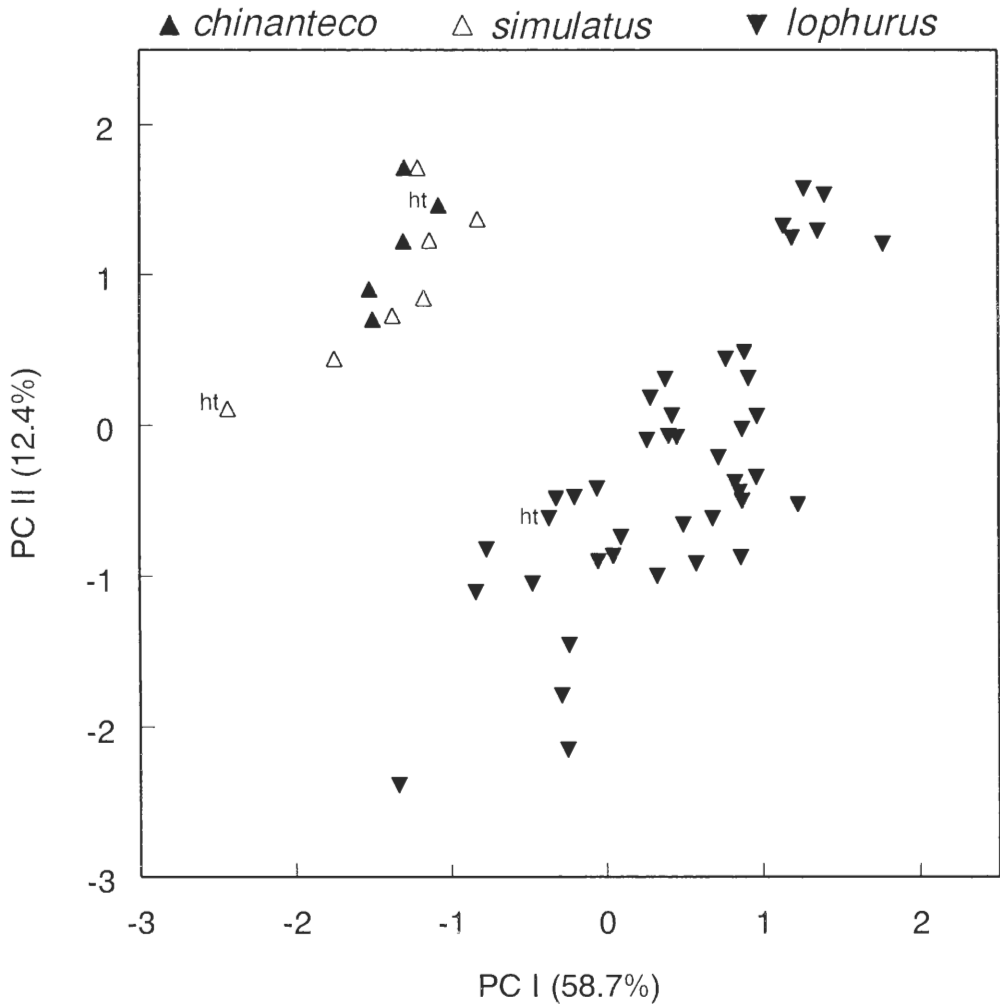


Fig. 5. Scatterplot of first and second principal components extracted from analysis of 19 log-transformed craniodental variables of intact specimens representing *Habromys lophurus* ($n = 42$) and the small taxa, *H. chinanteco* ($n = 5$) and *H. simulatus* ($n = 7$). The position of the type specimens of the respective taxa is indicated by "ht". See Table 3.

more robust molar rows and wider incisors of the former species (Table 4). Divergence between OTUs of *chinanteco* and *simulatus*, as revealed by UPGMA clustering using Mahalanobis distances between centroids, approximates the level of differentiation that subtends the more broadly drawn geographic samples of *H. lophurus* (Fig. 6).

Robertson & Musser (1976:2) observed that "The crania of *chinanteco* and *simulatus* are similar in size . . . but differ in

certain features." The "certain features" emphasized seem less satisfactorily diagnostic with the barely improved samples of *simulatus* series now at hand, $n = 7$ as compared with the three available to Robertson & Musser (1976). For one, the posterior termination of the incisive foramina—well anterior to the level of the M1s in *chinanteco* and near the middle of the M1s in *simulatus*—varies within each form and offers an inconsistent means for discrimination (Nor does such a difference actually characterize

Table 3.—Results of principal components analysis performed on intact specimens ($n = 55$) representing *Habromys lophurus* and the small species, *H. chinanteco* and *H. simulatus* (see Fig. 5).

Variable	Correlations	
	PC I	PC II
ONL	0.92	0.14
ZB	0.92	0.13
BZP	0.90	-0.01
IOB	0.09	0.56
BBC	0.20	0.48
BOC	0.79	0.14
HBC	0.47	0.00
LR	0.72	0.31
BR	0.62	0.54
LD	0.70	0.32
LIF	0.82	-0.23
BIF	0.70	0.36
LBP	0.63	0.17
BM1s	0.36	0.84
WMF	0.79	0.12
PPL	0.85	-0.04
CLM	0.83	-0.40
WM1	0.81	-0.41
BIT	0.81	-0.32
Eigenvalues	0.048	0.011
% Variance	58.1	12.8

the exemplars of *simulatus* [KU 83262] and *chinanteco* [KU 124129] Robertson & Musser selected for illustration [1976: Fig. 1]). A simple bivariate plot (LIF versus LD) that might reveal proportional contrast in lengths of the incisive foramen instead discloses broad overlap between the two species (Fig. 7). For another, they noted that specimens of *chinanteco* possess longer and narrower nasal bones. Although we did not measure nasal length per se, the strongly correlated dimension length of rostrum, relative to occipitonasal length, does not convey an unambiguous utility for separating the two species (Fig. 7). Finally, the “slightly more inflated” cranium of *chinanteco* finds little confirmation in certain breadth measurements (ZB, IOB, BBC, BOC, DBC) that would plausibly index such a specific contrast (Appendix 1).

Nor do means and ranges of most standard dimensions of the skin indicate that “externally, *chinanteco* is larger than *si-*

mulatus” (Robertson & Musser 1976: Table 1; also see Appendix 1). Of the specific differences they highlighted, only the absolutely and proportionally longer tail of *chinanteco* can be clearly verified with specimen data: mean = 109.2 mm, or approximately 121% of head and body length, in *chinanteco* versus a mean = 94 mm, or 106% of head and body length, in *simulatus* (Appendix 1). Caution is warranted in accepting the magnitude of this disparity, since sample sizes are too small to accurately typify such a large dimension, one exhibiting substantial allometric variation with age. Furthermore, the shorter mean tail length of *simulatus* is influenced by the exceptionally small values recorded for the type (87 mm) and paratype (78 mm) of the species, specimens collected a century ago. Still, these dimensions seem reasonable as inferred from remeasurement of tail length on the dry skins; moreover, the recorded tail lengths for *simulatus* collected recently by BYU field teams also average shorter than those of *chinanteco* (Appendix 1).

Habromys lepturus (Merriam 1898) and *Peromyscus ixtlani* Goodwin 1964.—Merriam (1898) described *Peromyscus lepturus* based on eight specimens from two localities on Cerro Zempoaltepec, Oaxaca, and at the time of Osgood’s (1909) revision, the species was still known only by Merriam’s original paradigm. While Merriam focused the comparisons of his new species with *P. guatemalensis*, Osgood recognized the fundamental similarities in cranial proportions and external traits that allied *lepturus* with *lophurus* and *simulatus*, a grouping that previewed the formal designation of a subgenus *Habromys* based on features of the male phallus (Hooper & Musser 1964).

Another specific relative of *lepturus*, *Peromyscus ixtlani* Goodwin (1964), was later described from Cerro Machín in the Sierra de Juárez, a north-south trending mountain system that is geographically close to the Sierra de Zempoaltepec in northcentral Oaxaca but geologically isolated from it. Goodwin listed the differentiat-

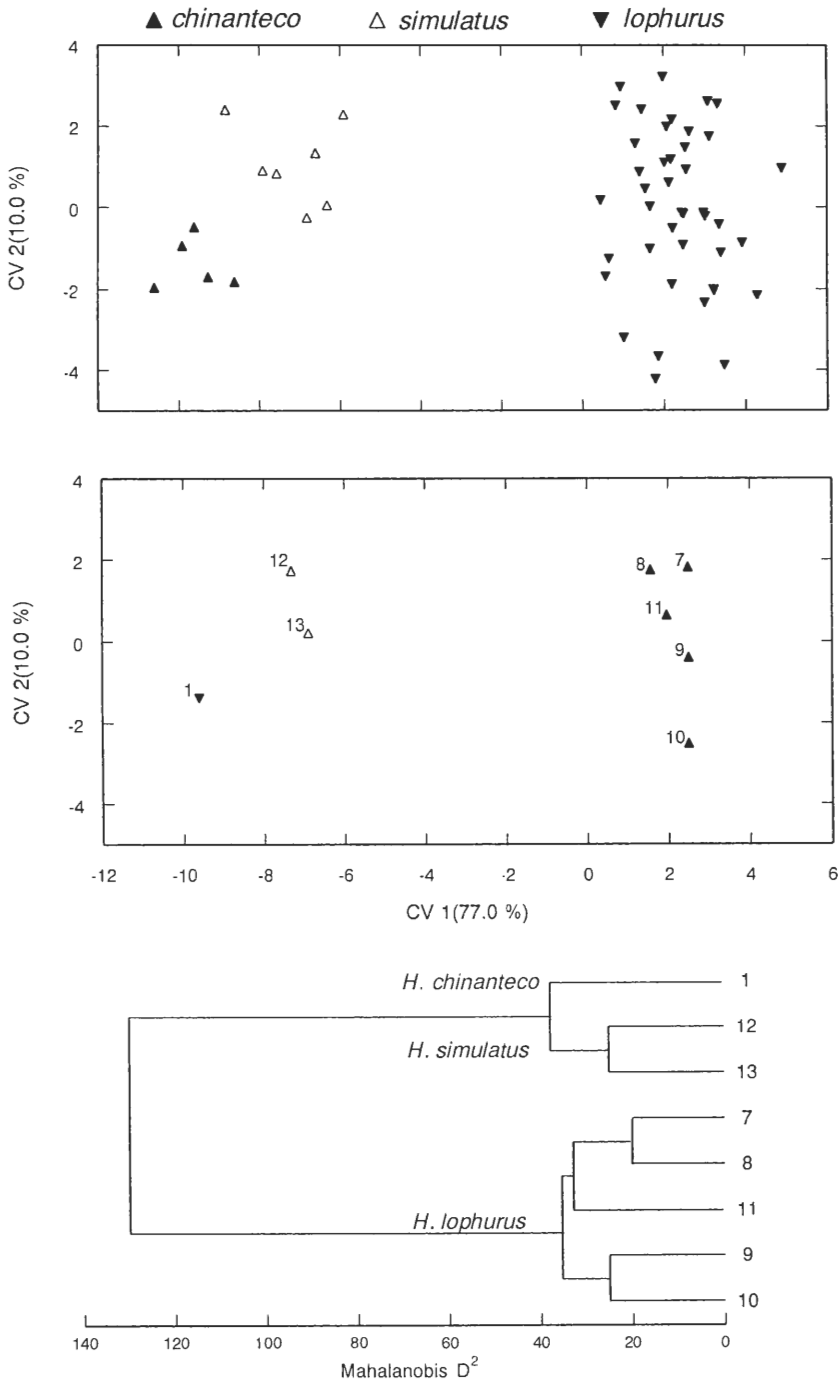


Fig. 6. Results of discriminant function analysis performed on 19 log-transformed craniodental variables as measured on 54 intact specimens representing eight samples of *Habromys lophurus* (OTUs 7–11) and the small taxa, *H. chinanteco* (OTU 1) and *H. simulatus* (OTUs 12, 13). Top, projection of individual specimen scores on first two canonical variates extracted; middle, projection of group centroids on first two canonical variates extracted; bottom, UPGMA phenogram based on Mahalanobis distances between the eight OTU centroids. The magnitude of morphometric differentiation between *H. chinanteco* and *H. simulatus* approximates that observed among the more widespread samples of *H. lophurus*. See Table 4.

Table 4.—Results of discriminant function analysis performed on intact specimens (n = 55) representing the eight OTUs of *Habromys lophurus* and the small species, *H. chinanteco* and *H. simulatus* (see Fig. 6).

Variable	Correlations	
	CV 1	CV 2
ONL	0.65	-0.46
ZB	0.70	-0.45
BZP	0.72	-0.25
IOB	-0.21	-0.45
BBC	-0.13	-0.46
BOC	0.61	-0.48
HBC	0.44	-0.26
LR	0.35	-0.51
BR	0.23	-0.49
LD	0.32	-0.39
LIF	0.77	-0.18
BIF	0.35	-0.68
LBP	0.34	-0.51
BM1s	-0.09	-0.60
WMF	0.58	-0.52
PPL	0.71	-0.41
CLM	0.95	-0.16
WMI	0.89	-0.24
BIT	0.76	-0.09
Canonical correlations	0.98	0.87
Eigenvalues	22.8	3.0
% Variance	77.0	10.0

ing features that persuaded him to recognize *ixtlani* as a species distinct from *lepturus*, notably a longer and more bicolored tail, absence of a dusky patch on the metatarsum, and overall larger size of the cranium and molars. Musser (1969) not only confirmed but amplified the consistency of the size and external differences between *ixtlani* and *lepturus*, yet ultimately elected (p. 17) to taxonomically acknowledge those dissimilarities as morphologically distinct but ecologically similar, montane subspecies. That he pointedly retained *ixtlani* as a well marked subspecies of *lepturus* is by itself instructive, given the era of revision and the prevailing custom to recognize slight but consistent (diagnostic) populational differences as subspecies.

The amount and constancy of craniodental differentiation between the two sets of montane populations are impressive in view of their geographic proximity and probable recency of their isolation. The sample from Cerro Zempoaltepec, *lepturus* proper, is clearly isolated from those of *lophurus* and *ixtlani* in plots of the first two canonical variates (cumulative variation = 90.5%) extracted from a nine-group dis-

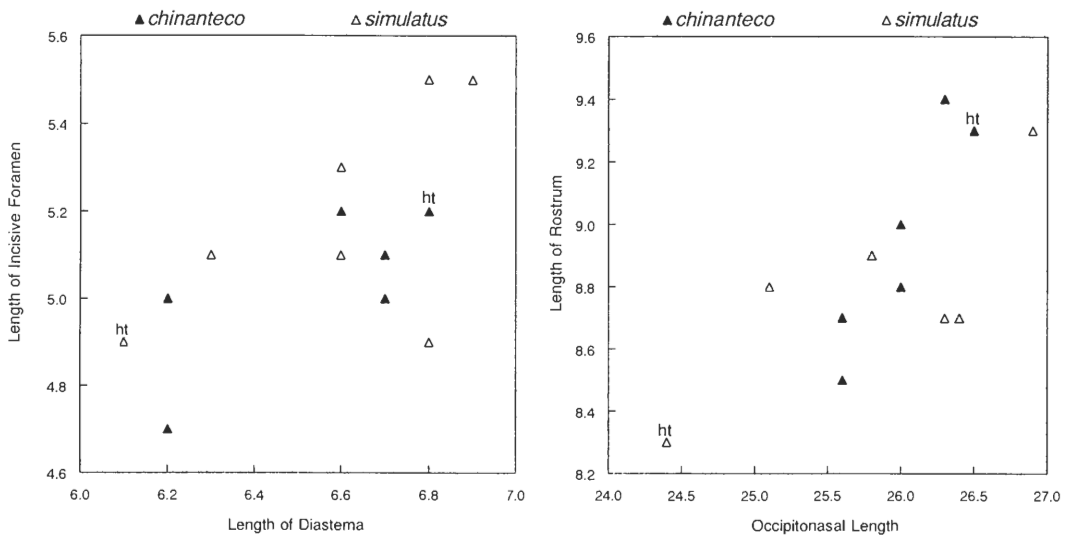


Fig. 7. Bivariate plots of select cranial dimensions (mm) relevant to the differential diagnosis of *Habromys chinanteco* from *H. simulatus*. Left, length of incisive foramen versus length of diastema; right, length of rostrum versus occipitonasal length (position of respective type specimens indicated by "ht"). See text for discussion.

Table 5.—Results of discriminant function analysis performed on intact specimens ($n = 191$) representing the nine OTUs of *Habromys lepturus ixtlani*, *H. l. lepturus*, and *H. lophurus* (see Fig. 8).

Variable	Correlations	
	CV 1	CV 2
ONL	-0.88	0.17
ZB	-0.72	0.14
BZP	-0.66	0.16
IOB	-0.73	0.09
BBC	-0.74	0.16
BOC	-0.75	0.22
HBC	-0.43	0.44
LR	-0.91	0.12
BR	-0.69	0.22
LD	-0.89	0.10
LIF	-0.68	-0.07
BIF	-0.56	0.26
LBP	-0.86	-0.16
BM1s	-0.66	0.17
WMF	-0.34	-0.09
PPL	-0.85	0.09
CLM	-0.78	-0.04
WM1	-0.87	0.09
BIT	-0.63	0.43
Canonical correlations	0.96	0.77
Eigenvalues	11.7	1.5
% Variance	79.9	10.6

criminant function analysis (Fig. 8). Only one of 27 specimens of *lepturus* was incorrectly placed with another group, OTU 10 of *lophurus*, according to a posteriori probabilities of group membership; percent correct assignments ranged from 56 to 71 for samples of *ixtlani* and from 20 to 60 for those of *lophurus*, with misclassified individuals occurring only among OTUs within each taxon. Greater size in all dimensions accounts for most separation between samples of *lepturus* and *ixtlani* in multivariate space (Table 5), a result consistent with Musser's (1969: Table 1) univariate comparisons of the two. Noteworthy are the stronger correlations that reflect the relatively longer rostrum (LR, LD), longer palate (LBP), and larger molars (LM1-3, WM1) of individuals of *ixtlani* compared with those of *lepturus* (Figs. 9, 10; Appendix 1). Although appearing morphologically intermediate to *lophurus* and *ixtlani* in

the canonical bivariate plot, OTU 5, representing *lepturus*, clearly links with OTUs of *ixtlani* based on Mahalanobis distances among centroids, albeit at a higher level than that observed among the widespread geographic samples of *lophurus* (Fig. 8).

In a discriminant function analysis restricted to samples of *ixtlani-lepturus* (OTUs 2-5), height of braincase emerges to contribute weakly to discrimination (not illustrated), reflecting the more vaulted cranial profile of *lepturus* (Fig. 10), in addition to the predominant influence of the aforementioned five variables. In this four-group morphometric comparison, no individual of *lepturus* (OTU 5) was misclassified with those of *ixtlani* (OTUs 2-4) in jack-knifed classifications according to posterior probabilities of group membership; misclassification of specimens among OTUs 2-4 of *ixtlani* ranged from 33 to 47 percent.

Qualitative traits.—Hooper (1958) segregated *lepturus* and *lophurus* from other *Peromyscus* species in his *Lepturus* Division, the taxonomic forerunner of the subgenus *Habromys* later named by Hooper & Musser (1964:12, type species = *Peromyscus lepturus* Merriam, 1898). The reality of *Habromys* as a distinct clade comparable to other *Peromyscus* subgenera (sensu Hooper 1968) was bolstered by Linzey & Layne (1969), who noted the unique complement of male accessory reproductive glands possessed by *lepturus*. Its particular traits were later confirmed and also verified as characteristic of *lophurus* by Carleton (1980), and Linzey & Layne (1974) reported the lack of an acrosomal hook on spermatozoa in these species as compared with other *Peromyscus* (sensu lato). As noted by Carleton (1989), however, the cardinal diagnostic features of the reproductive tract have yet to be confirmed for the smaller species assigned to *Habromys*. Variation within the material now available, although less than desirable in sample size and preservation, suggests that expanded analysis of this organ system is a profitable avenue of future systematic investigation.

Based on the two examples examined (CNMA 22439, 25908), *H. delicatulus* possesses a phallus like that described for *H. lepturus* and *H. lophurus* (Hooper 1958, Hooper & Musser 1964). Notable resemblances among the three species include the nonspinous epidermis of the glans penis, the absence of dorsal and ventral lappets, and the nearly terminal placement of the urinary meatus and correlative lack of a protrusible tip. The three also exhibit similar phallic proportions, especially the small size of the glans penis, its gradually tapering form from base to tip, and a baculum much longer than the body of the glans.

The single male of *H. delicatulus* with the proximal accessory reproductive glands preserved (CNMA 25908) clearly exhibits one trenchant feature of *Habromys* as documented by Linzey & Layne (1969) and Carleton (1980). The vesicular glands are greatly reduced, appearing as small straight diverticula that arise from the cephalic urethra, and are hidden in ventral view by the converging deferent ducts and stalk of the urinary bladder. Such a morphology strikingly contrasts with the large and arching vesicular glands, shaped like an inverted "J", observed in *Peromyscus sensu stricto* (Linzey & Layne 1969). The bulbourethral glands are moderately sized, comparable to those typical of *Peromyscus*. The specimen appears to be reproductively active, given the size of the gonads and distended condition of both caput and cauda epididymides. However, we cannot critically ascertain the presence or formation of other accessory glands due to the poor preservation and removal of the prepuce during specimen preparation.

The reproductive tract in two specimens of *H. simulatus* (BYU 15051, 15052) unexpectedly departs from the aforementioned species in two important traits. First, the surface of the glans penis is invested with minute spines that are closely packed and evenly distributed in size and density around the circumference. However, as in *delicatulus*, *lepturus*, and *lophurus*, the

glans penis of the two *H. simulatus* possesses a urinary meatus that opens nearly at the tip and lacks a protrusible tip and dorsal and ventral lappets. Moreover, size and conformation of the phallus are comparable: that is, short and relatively narrow, awl-shaped with a blunt tip, and the baculum longer than the body of glans. Dimensions, as measured on BYU 15051, are: bacular length = 4.5 mm (estimated since phallus not cleared and stained); glans length = 3.4 mm; glans width = 0.6 mm.

Second, a well defined, single pair of elongate (about 2.5 mm) preputial glands are clearly present in both BYU 15051 and 15052 of *H. simulatus*. Preputial glands have not been reported for the larger species, *H. lepturus* and *H. lophurus* (Linzey & Layne 1969, Carleton 1980), and we could not determine the presence or absence of preputials in *H. delicatulus*. We note that the animals dissected by those authors actually represent the populations found on Cerro Pelón, now called *H. lepturus ixtlani*; the complement of accessory glands characteristic of *lepturus* proper, type species of *Habromys*, remains to be confirmed.

Carleton (1980) identified another trait, the modal number of thoracic (13) and lumbar (7) vertebrae, that he interpreted as derived and posed as diagnostic of *Habromys* (based on examinations of *H. lepturus ixtlani* and *H. lophurus*). Other peromyscines and neotomines standardly possess the hypothesized ancestral ratio of 13 thoracics and 6 lumbar, and this is the count evident in the few available specimens of the small species, *H. delicatulus* (CNMA 22449, 22441) and *H. simulatus* (BYU 15050-15053).

Taxonomic recommendations.—We advise the retention of all named forms of *Habromys* as species. Although the Sierras de Zempoaltepec and Juárez are geographic neighbors in northcentral Oaxaca, the populations on those mountains (*lepturus* and *ixtlani*, respectively) are more strongly differentiated from one another than observed

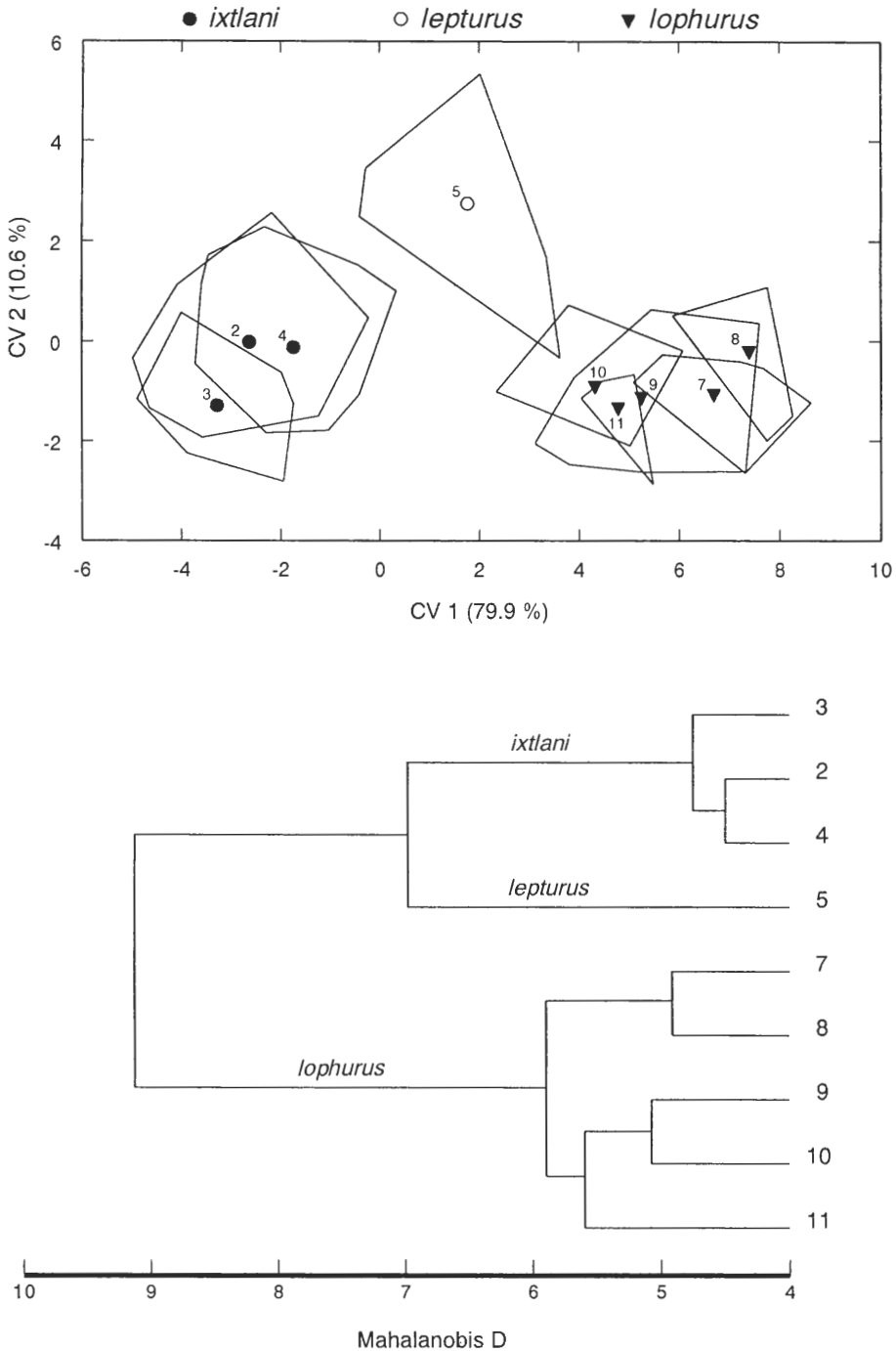


Fig. 8. Results of discriminant function analysis performed on 19 log-transformed craniodental variables as measured on 191 intact specimens representing nine samples of *Habromys lophurus* (OTUs 7–11) and the large taxa, *H. ixtlani* (OTUs 2–4) and *H. lepturus* (OTU 5). Top, projection of specimen scores on first two canonical variates extracted (polygons enclose maximal dispersion of individual scores around group centroids for each OTU); bottom, UPGMA phenogram based on Mahalanobis distances between the nine OTU centroids. See Table 5.

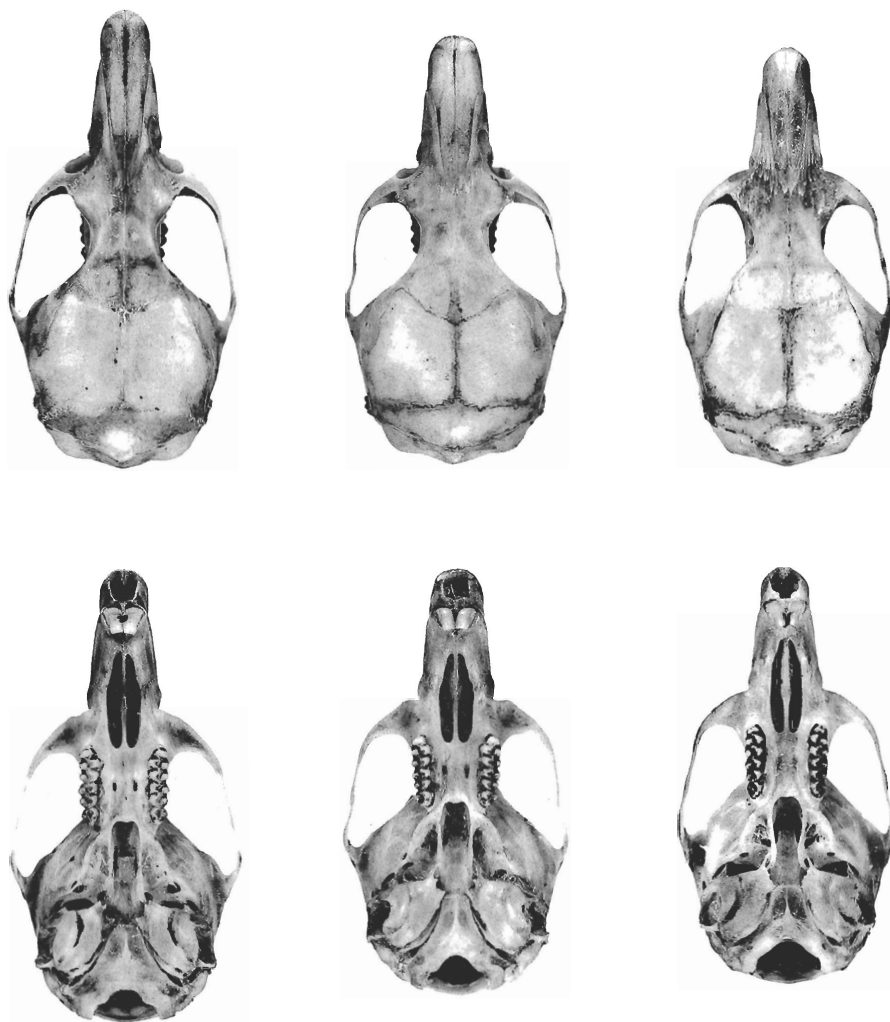


Fig. 9. Dorsal and ventral views (about 2 \times) of adult crania illustrating the three larger forms of *Habromys*. Left pair, *H. ixtlani* (MVZ 159729), a male from 5.2 mi NNE El Machín, Oaxaca; middle pair, *H. lepturus* (USNM 68619), a male from Cerro Zempoaltepec, Oaxaca; and right pair, *H. lophurus* (MVZ 98615), a male from Los Esesmiles, El Salvador.

among the more widely distributed samples of *H. lophurus* in mountains southeast of the Isthmus of Tehuantepec (Fig. 11). This morphological distinction reflects not only the consistently smaller size of *H. lepturus* but also its distinctive cranial shape (relatively shorter rostrum and bony palate, more arched cranium) and pelage traits (tail generally monocolored, presence of metatarsal patch) as compared with *H. ixtlani*. Studies should be conducted to determine

whether the level of genetic divergence between these montane forms concurs with their substantial morphological distinctiveness. And while their geographic proximity and phenetic similarity relative to other *Habromys* OTUs suggest that each is the other's nearest relative, this assumption too should be tested, for other congeneric species found in these mountains are known to be only distantly related. Characteristics of *Microtus umbrosus* (Sierra de Zempoalte-

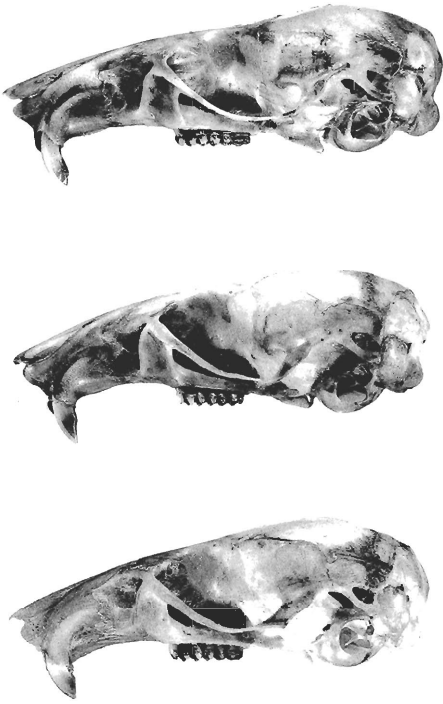


Fig. 10. Lateral view (about 2 \times) of adult crania illustrating the three larger forms of *Habromys*. Top, *H. ixtlani*; middle, *H. lepturus*; and bottom, *H. lophurus* (same specimens as in Fig. 9).

pec) and *M. oaxacensis* (Sierra de Juárez) do not support a sister-group relationship and instead underscore the potential of independent evolutionary histories of populations isolated in these neighboring mountain chains (Cervantes et al. 1994, 1997).

The overlapping pattern of craniodental variation in multivariate space and lower inter-locality distances exhibited among samples of *H. lophurus* suggest that only a single species ranges over Nuclear Central America. The samples from Chiapas, Mexico (OTUs 7, 8), consistently cluster apart from those collected farther south in the mountains of Guatemala and El Salvador (Fig. 8). This phenetic association supports the observations of Robertson & Musser (1976), who noted that the Chiapan examples of *H. lophurus* average slightly smaller in most dimensions. Although probably isolated from populations in the nearest Gua-

temalan cordilleras, we regard this slight distinction as intraspecific (geographic) variation and insufficient to warrant formal taxonomic recognition.

The case for the specific validity of *chinanteco* is admittedly weak. Its range in northern Oaxaca appears to be limited to cloud forest on the Caribbean watershed of the Sierra de Juárez; to date, the form has not been recovered at sites situated on interior slopes of that sierra, places in pine-oak forest where *H. ixtlani* has been collected (Musser 1969). The geographic presence of *chinanteco* in the Oaxacan highlands thus mirrors the distribution of *H. simulatus* in subtropical cloud forest along the eastern slopes of the Sierra Madre Oriental (Fig. 12). The few examples of *chinanteco* display appreciable morphological overlap with the few available of *H. simulatus*, and most traits advanced for its diagnosis fail to provide clear discrimination between the two taxa. Nevertheless, the characteristic of a relatively and absolutely longer tail in *chinanteco*, a cardinal feature of its diagnosis and separation from *H. simulatus*, cannot be controverted with the material at hand. In addition to appeal to other data such as molecular and chromosomal information, the distinctive phallic traits reported above for *H. simulatus* promise a firmer basis for deciding their synonymy if these are found also to characterize specimens of *chinanteco*. The status of *chinanteco* as species or junior synonym of *H. simulatus* should be argued on incontrovertible evidence. In view of the meager numbers available and the different mountain systems these taxa occupy, we adopt a conservative course and shall leave the matter to future systematic investigation.

The recognition of *H. simulatus* as species is secure, aside from the unresolved issue of whether it should subsume the populations described as *chinanteco*. However, vouchered documentation of its geographic range requires amplification, especially in light of the report by León-Paniagua & Romo-Vázquez (1993) of *Peromyscus* aff.

simulatus in the Sierra de Taxco, Guerrero, a southern spur of the Cordillera Neovolcanica.

Habromys is currently viewed as a genus closely allied to *Podomys* and *Neotomodon*, and more distantly related to *Peromyscus* proper (Carleton 1980, 1989). A similar phyletic affinity among the first three taxa is supported by other systematic evidence, although its cladistic stature with regard to species of *Peromyscus* and consequent sufficiency to warrant generic recognition are disputed (e.g., Stangl & Baker 1984). Carleton (1980:127, 1989:128) has emphasized the need for expanded anatomical surveys and critical reinterpretation of character homologies for certain of the character systems applied relatively recently to questions of muroid systematics and phylogeny, particularly those of the reproductive system. *Habromys* appears to be an excellent candidate for such investigation, the results of which would do much to clarify the monophyly of included species relative to *Peromyscus* and other genus-group kin. The structure of the phallus and complement of accessory glands reported here for the smaller species *H. delicatulus* and *H. simulatus* reveal greater variability in the pivotal reproductive features on which the subgenus was founded (Hooper & Musser 1964) and upon which its phylogenetic diagnosis and generic status were argued (Carleton 1980, 1989). Or perhaps this variation raises doubts only about the proper assignment of Osgood's (1904) *simulatus* to the genus-group taxon. Whichever the case, improved characterization of the reproductive tract morphology of the small species assigned to *Habromys* must draw upon more and better preserved specimens.

Apart from the disagreement over details of cladistic branching and taxonomic rank, the above mentioned phylogenetic studies have improved little upon Hooper's (1968: 65) impression that "They [species of *Habromys*] appear to be relict taxa, which jointly may date to an early stage in the evolution of the genus" (or tribe sensu

Carleton 1989). As presently understood, the taxon includes some of the less well known, systematically and biologically, small Neotropical rodents. Only *H. ixtlani* is represented in collections in series sufficient to appreciate nongeographic variation. The inadequately small samples of *H. simulatus* and *H. chinanteco* clearly hinder decisive interpretation of their status as one or two species.

Phyletic Diversification Within *Habromys* And Other Mesoamerican Small Mammals

The geographic occurrence of *Habromys* is disjunct, conforming to naturally discontinuous highland forests from southern Mexico, through Guatemala, to El Salvador and probably Honduras (Figs. 11, 12). Collectively, species of *Habromys* have been captured at sites ranging from 1830 to 3150 meters in altitude, and descriptions of collection sites consistently emphasize the cool, moist character of the forest, usually with a lush herbaceous ground cover, dense carpets of mosses and lichens, and abundant bromeliads and other epiphytes (Goldman 1951, Musser 1969, Carleton & Huckaby 1975, Robertson & Musser 1976). In Oaxaca, collecting localities of *Habromys* fall within Cloud Forest (1250–2012 m) and Pine-Oak Forest (2012–3000 m), as those life zones are regarded by Binford (1989) for the state's avifauna. The type locality of the newly named *H. delicatulus* also fits this pattern, restricted to a cool forested enclave on a north-facing slope of mountains fringing the southern Mesa Central. And León-Paniagua & Romo-Vázquez (1993) reported *Peromyscus* aff. *simulatus* from the vicinity of Taxco, Guerrero, about 2200–2400 m in a steep ravine sheltered by oak forest. The latter two discoveries highlight the likelihood of greater taxonomic differentiation among such montane rodents than presently recognized, and invite not only additional biological survey of southern México's geologically and biotically intricate mountains but also renewed revi-

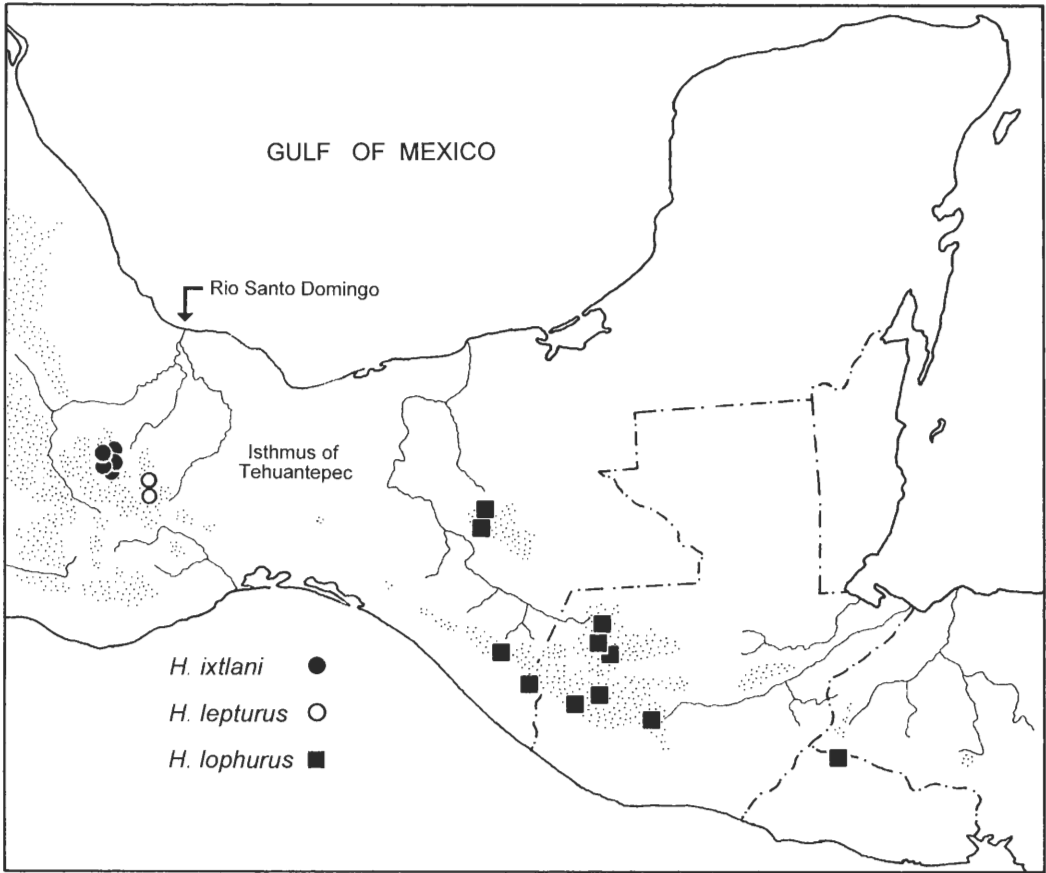


Fig. 11. Map of northern Mesoamerica, illustrating the geographic distributions of the larger species of *Habromys* as based on specimens examined. *Habromys lophurus* is the only species so far known from highlands to the east and south of the Isthmus of Tehuantepec. *Habromys lepturus* and *H. ixtlani*, along with the three smaller species (Fig. 12), are known from restricted mountain ranges to the west and north of the Isthmus. Stippled areas indicate regions above 2000 meters.

sionary attention to the small terrestrial mammals distributed among them.

In view of their ecological restriction to montane humid-forest associations, the distribution of *Habromys* taxa intelligibly corresponds to major mountainous systems of Mesoamerica: *H. delicatulus* in a northern spur of the Cordillera Neovolcanica; *H. simulatus* and *H. chinanteco* on the gulf-facing flanks of the Sierra Madre Oriental and Sierra de Juárez, respectively; *H. lepturus* and *H. ixtlani* in different ranges of the Oaxacan Highlands; and *H. lophurus* in the highlands of Nuclear Central America. Such physiographic complementarity, and

its general agreement with patterns of endemism and vicariance distilled for other Mesoamerican vertebrates (Duellman 1966, Wake & Lynch 1976, Wake 1987, Good 1988, Hernández-Baños et al. 1995, Campbell 1999), suggest that geologic, climatic, and biotic changes of the late Cenozoic have left their imprint in the diversification of species of *Habromys*. In particular, the possible sister group relationship of *H. lophurus* and *H. lepturus*-*H. ixtlani* and its vicariant genesis concordant with the barrier imposed by the Isthmus of Tehuantepec merit exploration with other data. Our conjecture is circumstantial, shaped mostly by

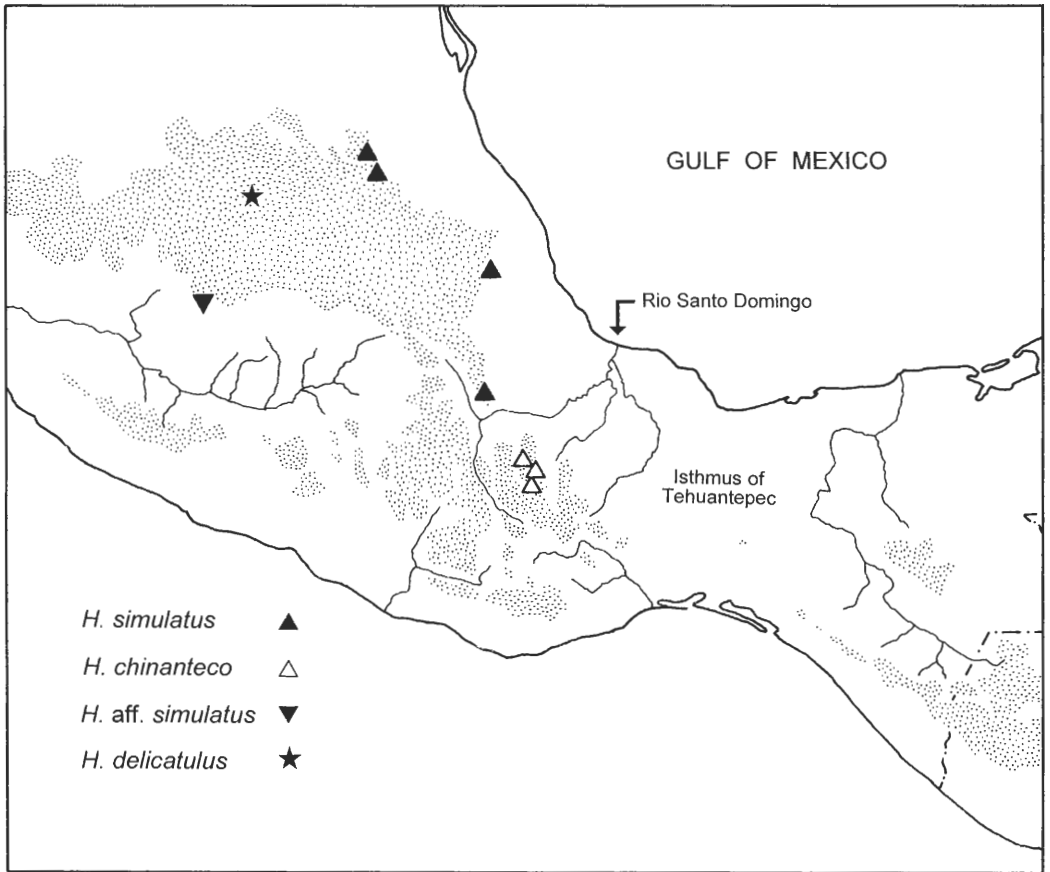


Fig. 12. Map of southern México, illustrating the geographic distributions of the smaller species of *Habromys* as based on specimens examined. *Habromys delicatulus* is the first species of the genus described from the Cordillera Neovolcanica, but León-Paniagua & Romo-Vázquez's (1993) report of *H. aff. simulatus* from the Sierra de Taxco, Guerrero, anticipated documentation of the group's presence in these mountains. *Habromys simulatus* and *H. chinanteco* occupy moist forests along Gulf-facing slopes of Mexico's eastern versant, the former in the Sierra Madre Oriental to the north of the Río Santo Domingo, and the latter in the Sierra de Juárez to the south. Stippled areas indicate regions above 2000 meters.

their hierarchical levels of morphometric divergence and by analogy with biogeographic patterns recently advanced for other small mammals confined to cool and moist highland forest in Mesoamerica (Sullivan et al. 1997, 2000; Woodman & Timm 1999).

Woodman & Timm (1999:30) remarked that "In general, the isthmus [of Tehuantepec] does not appear to have been regarded as a major barrier to most small mammals . . ." Their point is not strictly true, as the following examples demonstrate, but holds import in a refocused context. Baker (1963:246) actually had featured the Isth-

mus throughout his review of Mesoamerican small mammal distributions and underscored its significance as the first point of his overall summary: "The hilly tropical lowland of the narrow Isthmus of Tehuantepec provides a major break in present-day mammalian distribution in Middle America." On a continental scale, Wilson (1974) noted the strong association between high species density and high topographic relief, and his isocontours of greatest species density in northern Mesoamerica are localized over the highlands on either side of the Isthmus of Tehuantepec (although the isthmus

was not specifically mentioned). Both Hooper (1952) and Choate (1970) did specifically implicate the Isthmus of Tehuantepec as a primary fission zone in the earliest radiation of *Reithrodontomys* and *Cryptotis*, respectively, perhaps accounting for the initial evolutionary split between the subgenera *Reithrodontomys* and *Aporodon* on the one hand and for driving speciation within the *Cryptotis mexicana* species group on the other. And Hooper (1952:79) was well aware that "The low country of the Isthmus of Tehuantepec is a partial, if not complete, barrier to these highland forms [subspecies of *Reithrodontomys sumichrasti*]," and that (p. 170) "*R[eithrodontomys] m[icrodon] albilabris* is isolated from *R. m. microdon* by the Isthmus of Tehuantepec and by other arid lowlands." These examples convey appreciable regard for the Isthmus as a distributional divide, but, in general, those systematists of the middle 1900s who offered historical zoogeographic reconstructions preferentially emphasized its barrier effect in their divisions of subspecies (also see next section).

Although not disregarded by mammalogists, consideration of the Isthmus in taxonomic studies of small montane mammals does appear understated compared with the preeminent biogeographic role attributed to those dry lowlands in other vertebrate groups (Duellman 1960, 1966; Savage 1982; Wake 1987; Good 1988; Binford 1989; Flores-Villela 1993; Campbell 1999; Watson & Peterson 1999). Binford (1989) repeatedly emphasized the geographic impassability interposed by the lowland tropical forests and drier climate of the Isthmus for the dispersal of bird species restricted to cloud forest and pine-oak habitats and the consequent high levels of endemism on either side of it. Good (1988) considered the vicariant significance of the Isthmus in interpreting the radiation of certain highland genera of gerrhonotine lizards with species clades distributed on either side of it. Flores-Villela (1993) regarded the Isthmus barrier and rich endemism of pine-oak and

cloud forest herps in mountains to the west and east as logically interrelated.

In the context of such Mesoamerican biogeographic investigation, Woodman & Timm's (1999) observation exposes the rare cladistic documentation of related mammalian species pairs in mountains bordering the Isthmus of Tehuantepec and the explicit invocation of the drier isthmian lowlands as the vicariant barrier impelling their initial geographic separation and eventual speciation. In a phylogenetic study of small-eared shrews, genus *Cryptotis*, they provided such cladistic evidence for the relationship of *C. goldmani* and the species pair *C. goodwini*-*C. griseoventris* and postulated their evolutionary divergence coincident with the isthmian lowlands. Other possible vicariant pairs among small, montane dwelling rodents distributed over the same region include *Oryzomys chapmani*-*O. saturator* (Musser & Carleton 1993) and [*Habromys lepturus*-*H. ixtlani*]-*H. lophurus* (this study). The most persuasive evidence for the interplay of Mesoamerican topography and phyletic diversification among montane rodents issues from the recent studies of Sullivan et al. (1997, 2000), who applied cytochrome *b* data to the understanding of phylogeographic relationships within the *Peromyscus aztecus* and *Reithrodontomys sumichrasti* complexes. In both cases, their trees divulged an early divergence of populations inhabiting highlands to the east of the Isthmus of Tehuantepec from those in highlands to the west and north. Although the differentiation of these trans-isthmian moieties is not recognized at the specific level in current taxonomy, the weight of their evidence inescapably points toward that conclusion.

Of the 76 small terrestrial mammals and seven mountainous regions considered here (Table 6), the greatest densities of species occur in the highlands that flank the Isthmus of Tehuantepec, the Oaxacan Highlands and Nuclear Central America. The latter region also contains a large percentage of endemic species, over half according

to our current taxonomic understanding. Comparably high levels of endemism, albeit fewer species, are recorded for the Cordillera Neovolcanica and the Talamancan Highlands; the fewest species and fewest endemics occur in sections of the Sierra Madre del Sur. The smaller number of montane species tabulated for the Talamancan Highlands of southern Central America contradicts the general continental trend in diversity disclosed for all Mammalia (Simpson 1964, Wilson 1974, Kaufman 1995). The depression in these southern highlands reflects our omission of chiropteran species, whose abruptly greater densities in the Neotropics heavily weight the continental gradient of increased species richness at lower latitudes (Wilson 1974, Kaufman 1995). Otherwise, the distribution of species richness and foci of endemism among terrestrial small mammals correspond generally to the patterns observed for montane species of Mesoamerican amphibians and birds (Duellman 1966, Hernández-Baños et al. 1995, Campbell 1999); for certain groups, such as plethodontid salamanders, these biodiversity landmarks correspond closely (Wake & Lynch 1976).

Many of the endemics within the Oaxacan Highlands or Nuclear Central America—such as *Habromys lepturus* and *Microtus umbrosus* in the former or *Cryptotis griseoventris* and *Peromyscus zarhynchus* in the latter—are confined to discrete subregions within the larger biogeographic province recognized, narrow endemics or microendemics in the terminology of some (Hernández-Baños et al. 1995 and Campbell 1999, respectively). Some of these microendemics are hypothesized to be (e.g., *Cryptotis griseoventris*-*C. goodwini*, Woodman & Timm 1999), or suspected to be (e.g., *Peromyscus grandis*-*P. guatemalensis*-*P. zarhynchus*, Huckaby 1980), members of clades that have locally speciated within the principal biogeographic unit. Alternatively, subsequent research may reveal that certain “microendemics” (e.g., *Sorex sclateri* or *Neotoma chrysomelas*) are in-

stead junior synonyms of more broadly ranging species. Nonetheless, the decrease in diversity or absolute endemism that results from such revisionary synonymies will be overcompensated by the increase in valid species yet to be identified through systematic review of the many widely distributed, polytypic composites among these families (see below): the distribution of species richness and patterning of endemism evident among Mesoamerican shrews and rodents, as tabulated here, will remain robust in the face of such future taxonomic study.

We agree with the suggestion of Watson & Peterson (1999:587), who observed that diversity patterns at the regional level of Mesoamerica can be partly explained in terms of singular historical factors that have served to augment speciation, rather than solely as correlates of general latitudinal or climatic trends operating at a continental scale. For small terrestrial mammals, we would extend their observation and say that such patterns will eventually be shown to be more readily explainable by the former. The occurrence of these shrews and rodents in humid montane forests, coincident with the complex tectonic activity and profound climatic oscillations within the region over the middle to late Cenozoic (e.g., see overview and numerous citations in Campbell 1999), has offered an ideal evolutionary setting for recurrent fragmentation of biotas, differentiation of allopatric isolates, and secondary dispersion and overlap.

In particular, the greater species diversity and high degree of endemism tallied for Nuclear Central America seem consistent with its intermediate geographic location, a serendipitous biogeographic intersection intermittently accessible to groups of more northern or southern affinity at different periods within the Cenozoic. Most species of shrews and small rodents within Nuclear Central America appear to share common ancestry with those in Mexico's southern mountains, especially the Oaxacan Highlands (examples listed above). The pheno-

Table 6.—Occurrences^{1 a-kk} of terrestrial small mammals (Soricidae, Heteromyidae, Muridae) restricted to humid montane regions of Mesoamerica.

Species	Mountain System						
	Cor- dillera Neovol- canica	S.M. Oriental	Oaxacan High- lands	S.M. del Sur-West	S.M. del Sur-East	Nuclear Cent. Amer	Tala- mancan High- lands
Insectivora: Soricidae							
<i>Cryptotis alticola</i> ^{jj}	X						
<i>C. endersi</i> ⁱ							X
<i>C. goldmani</i> ^{jj}			X	X	X		
<i>C. goodwini</i> ^{jj}						X	
<i>C. gracilis</i> ^{hh}							X
<i>C. griseoventris</i> ^{jj}						X	
<i>C. hondurensis</i> ^{hh}						X	
<i>C. magna</i> ⁱ			X				
<i>C. merriami</i> ⁱⁱ						X	X
<i>C. mexicana</i> ^{i, jj}		X	X			X	
<i>C. nelsoni</i> ^{jj}		X					
<i>C. nigrescens</i> ⁱⁱ							X
<i>C. obscura</i> ^{jj}		X					
<i>C. parva</i> ^t	X	X	X		X	X	X
<i>C. peregrina</i> ^{kk}			X				
<i>C. phillipsi</i> ^{kk}					X		
<i>Sorex macrodon</i> ^u		X					
<i>S. oreopolus</i> ^u	X						
<i>S. saussurei</i> ^u	X	X	X	X	X	X	
<i>S. sclateri</i> ^u						X	
<i>S. stizodon</i> ^u						X	
<i>S. ventralis</i> ^u		X	X		X		
<i>S. veraepacis</i> ^u			X	X	X	X	
Rodentia: Heteromyidae							
<i>Heteromys nelsoni</i> ^{bb}						X	
<i>H. oresterus</i> ^{aa}							X
Rodentia: Muridae							
<i>Habromys chinanteco</i> ^e			X				
<i>H. delicatulus</i> ^e	X						
<i>H. ixtlani</i> ^e			X				
<i>H. lepturus</i> ^e			X				
<i>H. lophurus</i> ^e						X	
<i>H. simulatus</i> ^e		X					
<i>Megadontomys cryophilus</i> ^s			X				
<i>M. nelsoni</i> ^d		X					
<i>M. thomasi</i> ^s				X			
<i>Microtus guatemalensis</i> ^o						X	
<i>M. mexicanus</i> ^o	X	X	X		X		
<i>M. oaxacensis</i> ^l			X				
<i>M. quasiater</i> ^r		X					
<i>M. umbrosus</i> ^k			X				
<i>Nelsonia goldmani</i> ⁱ	X						
<i>Neotoma chrysomelas</i> ⁿ						X	
<i>Neotomodon alstoni</i> ^{gg}	X						
<i>Oligoryzomys vegetus</i> ^f							X
<i>Oryzomys asphrastus</i> ^v							X
<i>O. chapmani</i> ^v		X	X	X	X		

Table 6.—Continued.

Species	Mountain System						
	Cor- dillera Neovol- canica	S.M. Oriental	Oaxacan High- lands	S.M. del Sur-West	S.M. del Sur-East	Nuclear Cent. Amer.	Tala- mancan High- lands
<i>O. devius</i> ^m							X
<i>O. rhabdops</i> ^y						X	
<i>O. saturator</i> ^y						X	
<i>Peromyscus aztecus</i> ^c		X	X	X	X	X	
<i>P. baetae</i> ^{b,cc}		X	X	X	X	X	
<i>P. furvus</i> ^w		X					
<i>P. grandis</i> ^s						X	
<i>P. guatemalensis</i> ^b						X	
<i>P. hylocetes</i> ^{c,ee}	X						
<i>P. mayensis</i> ^c						X	
<i>P. levipes</i> ^{b,cc}	X	X					
<i>P. megalops</i> ^s			X	X	X		
<i>P. melanocarpus</i> ^s			X				
<i>P. melanotis</i> ^{d,v}	X	X					
<i>P. melanurus</i> ^s					X		
<i>P. winkelmanni</i> ^{dd}				X ²			
<i>P. zarhynchus</i> ^s						X	
<i>Reithrodontomys brevirostris</i> ¹						X	X
<i>R. chrysopsis</i> ^p	X						
<i>R. creper</i> ^r							X
<i>R. mexicanus</i> ^p		X	X			X	X
<i>R. microdon</i> ^p	X		X			X	
<i>R. rodriguezii</i> ^p							X
<i>R. sumichrasti</i> ^p	X	X	X	X	X	X	X
<i>R. tenuirostris</i> ^a						X	
<i>Rheomys mexicanus</i> ^{ff}			X		X		
<i>R. raptor</i> ^{ff}							X
<i>R. thomasi</i> ^{ff}						X	
<i>R. underwoodi</i> ^{ff}							X
<i>Scotinomys teguina</i> ^a						X	X
<i>S. xerampelinus</i> ^a							X
# species	14	20	24	10	14	29	18
# endemics	7	7	9	1	2	17	9
% endemism	50.0	35.0	37.5	10.0	14.3	58.6	50.0

¹ a-kk Distributional sources: a, Arellano & Rogers 1994; b, Bradley et al. 2000; c, Carleton 1979; d, Carleton 1989; e, Carleton & Huckaby 1975; f, Carleton & Musser 1995; g, Carleton et al., this study; h, Castro-Campillo et al. 1999; i, Choate 1970; j, Engstrom et al. 1992; k, Frey & Cervantes 1997a; l, Frey & Cervantes 1997b; m, Gardner 1983; n, Hall 1981; o, Hoffmann & Koepl 1985; p, Hooper 1952; q, Hooper 1972; r, Hopp & Rogers 1994; s, Huckaby 1980; t, Jones & Genoways 1970; u, Junge & Hoffmann 1981; v, Martinez-Coronel et al. 1991; w, Martinez-Coronel et al. 1997; x, Musser 1964; y, Musser & Carleton 1993; z, Ramirez-Pulido et al. 1991; aa, Rogers & Rogers 1992a; bb, Rogers & Rogers 1992b; cc, Schmidly et al. 1988; dd, Smith et al. 1989; ee, Sullivan & Kilpatrick 1991; ff, Voss 1988; gg, Williams et al. 1985; hh, Woodman & Timm 1992; ii, Woodman & Timm 1993; jj, Woodman & Timm 1999; kk, Woodman & Timm 2000.

² The purported presence of *Peromyscus winkelmanni* in mountains both to the west (Michoacan, Sierra de Coalcoman) and east (Guerrero, Sierra Madre del Sur) of the Río Balsas seems improbable. We have tried unsuccessfully to locate and confirm the identification of the specimens (not listed by museum number) from near Filo de Caballo, Guerrero, that have served as the basis for reports on the species' karyology, systematic relationships, and vicariant biogeography (Smith et al. 1989, Sullivan & Kilpatrick 1991, Sullivan et al. 1997). Until these specimens resurface or the site is revisited, the presence of *P. winkelmanni* in the Sierra Madre del Sur, and its import for past biotic connections across the arid basin of the Río Balsas, should be viewed as suspect.

gram of faunal similarity suggests such a sequence of past biotic connections and divulges a hierarchy of area relationships (Fig. 13A) similar to that derived by Sullivan et al. (1997) for species and populations of the *Peromyscus aztecus* group (the distribution of this complex does not include the Talamancan Highlands). Some species in Nuclear Central America, on the other hand, clearly indicate former continuity of populations with the Talamancan Highlands—e.g., *Cryptotis merriami* (Woodman & Timm 1993), *Reithrodontomys brevirostris* (Jones & Genoways 1970), and *Scotinomys teguina* (Hooper 1972)—or the specifically distinct elements within each highland area are hypothesized to form a sister group—i.e., *Rheomys thomasi*-*R. raptor* (Voss 1988). Parsimony analysis of endemism emphasizes this area relationship (Fig. 13B), a result predictable from the sharing of those aforementioned species. Few montane shrews or rodents seem to share nearest common ancestry with lowland forms, a cladogenetic pattern that has been identified for the Mesoamerican highland herpetofauna (Savage 1982). Possible mammalian examples include *Oryzomys rhabdops*, a species thought to be most closely related to a lowland form such as *O. alfaroi* or *O. rostratus* (Carleton & Musser, in litt.), and *Cryptotis merriami*, perhaps closely related to *C. mayensis* of the Yucatan Peninsula (Woodman & Timm 1993). Rigorous phylogenetic investigations of montane small mammals are regrettably few to amplify these casual impressions of historical biogeography or to appraise the relative importance of northern versus southern origins of the component taxa that compose current montane biotas within Mesoamerica, the studies of Voss (1988), Sullivan et al. (1997, 2000), and Woodman & Timm (1999) providing noteworthy exceptions.

The foregoing consideration of patterns of diversity and area relationship requires several obvious caveats apropos our current knowledge of distribution and taxonomy of

small terrestrial mammals in Mesoamerica. Four are paramount.

(1) The a priori circumscription of the seven regions (Table 6, Fig. 13) as analyzable biogeographic units or areas of endemism poses issues of definability and comparability on both geographical and ecological scales. Such procedural questions have provoked much debate over deciding the actual distributional congruence of taxa and distilling historically meaningful areas of endemism (e.g., see Harold & Mooi 1994, Andersson 1996, Humphries & Parenti 1999, and references cited by each). The evidence for the seven humid montane districts as areas of endemism for small mammals remains largely circumstantial, but their precedence as such is jointly persuasive: they have drawn recognition, exactly or partly, in the early descriptive biogeographic literature on Mesoamerican mammalian distributions (Baker 1963, Ryan 1963); they have received greater or lesser attention in revisionary studies of taxa broadly distributed over Mesoamerica (Hooper 1952; Choate 1970; Carleton 1979; Huckaby 1980; Sullivan & Kilpatrick 1991; Woodman & Timm 1999, 2000); they have been hierarchically delineated in recent phylogeographic studies of small, co-distributed rodents (Sullivan et al. 1997, 2000); and the same or similar ecophysiological regions repeatedly appear in biogeographic commentary on other Mesoamerican organisms (Duellman 1966, Savage 1982, Wake 1987, Good 1988, Hernández-Baños et al. 1995, Campbell 1999, Morrone et al. 1999).

Still, discrepancies are apparent in how these physiographic areas have been perceived by biogeographers of different vertebrate groups. Noteworthy is the contrast in the southern delimitation of the Sierra Madre Oriental region as usually envisioned by mammalogists (Baker 1963, Fa & Morales 1993) versus that as circumscribed by herpetologists (Wake & Lynch 1976, Campbell 1999) and ornithologists (Hernández-Baños et al. 1995). The former

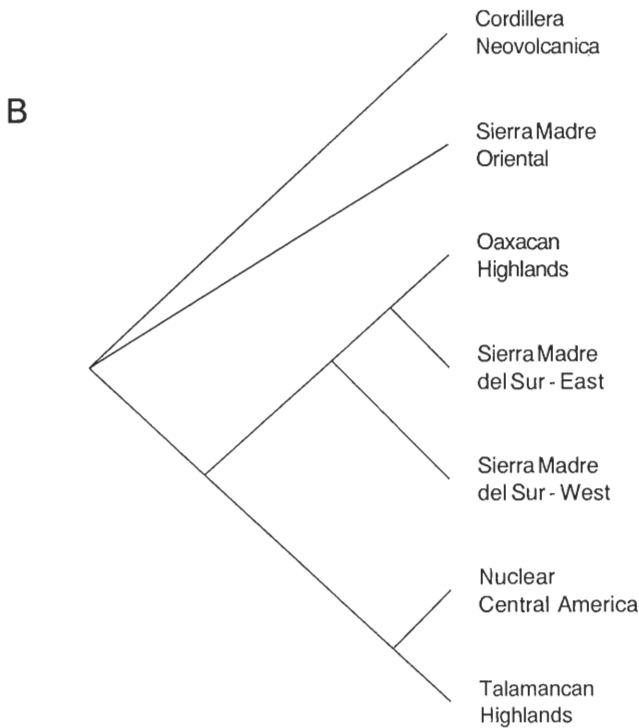
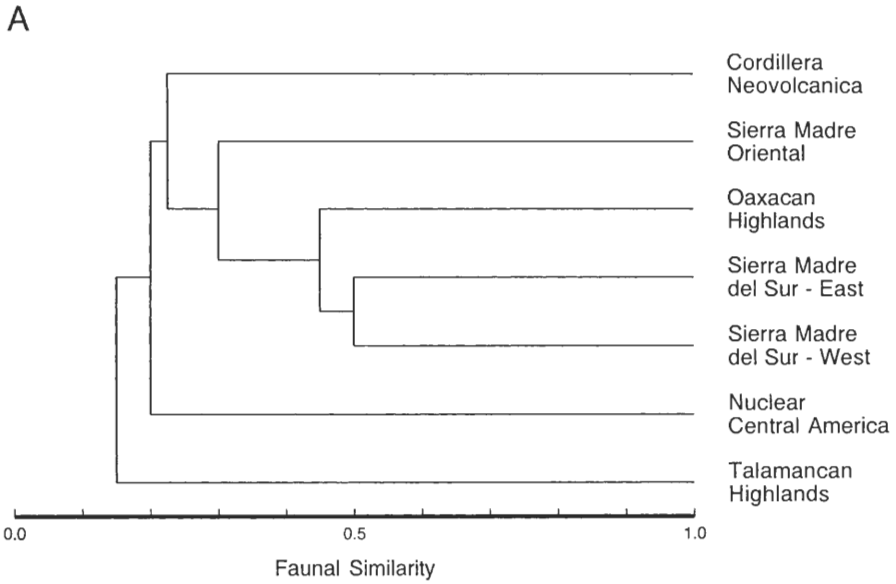


Fig. 13. Two interpretations of area relationships based on the geographic occurrences of small terrestrial mammals restricted to montane humid-forest associations in Mesoamerica (Table 6). A, Phenogram of faunal similarity produced from nearest-neighbor clustering of Jaccard's Index (coefficient of cophenetic correlation = 0.926, $P < 0.001$). B, Shortest tree (length = 87) derived from parsimony analysis of endemicity (consistency index, excluding uninformative taxa, = 0.61; retention index = 0.54).

have included the bordering cordilleras of the Mexican Plateau only to the vicinity of the eastern reaches of the Cordillera Neovolcanica, whereas the latter extend the biogeographic province farther south to include the Sierras de Juárez and Zempoaltepec of northern Oaxaca. Ecological considerations, as much as or more than physiographic ones, may bear on these differing interpretations of the limits of the Sierra Madre Oriental as an area of endemism. For example, the Sierra Madre Oriental inclusive of humid montane forests, as identified here and in other studies, already conflates the notions of physiographic space and biotic community and introduces definitional ambiguities (see Andersson 1996).

Future researchers will undoubtedly improve these area definitions, accepted here as (loosely) predefined, and correct attendant inconsistencies and assumptions as they apply to montane small mammals. The seven mountain regions are probably coarse biogeographic groupings that should be subdivided more in line with those identified for the Mesoamerican avifauna, as a basis for initially mapping vouchered specific occurrences and then discerning meaningful biogeographic units (Hernández-Bañón et al. 1995). For many small mammals, however, the distributional baseline and taxonomic framework do not match those available for Neotropical ornithology. Refinement of area definitions thus requires much basic attention to the insufficiencies identified in the next two points.

(2) Recognizing congruence in geographic ranges and areas of endemism hinges foremost on the empirical foundation of species distributions. Levels of collecting effort and the field sampling methods employed are implicitly assumed to be comparable in deriving the species tallies used to compute faunal resemblances. For the small mammals in question, we know that such biological survey and vouchered documentation within and among these highlands are grossly uneven and incomplete. The omission of at least some naturally oc-

curing species from a given region is probable, and the status of rarely collected species as broadly or narrowly distributed within it is uncertain. Additional field inventory is the obvious prescription, emphasizing elevational transects where continuous forest remains, together with intensive site surveys to document the resident montane mammals. The recent investigations in northern Oaxaca by Briones-Salas et al. (2001) and Sánchez-Cordero (2001) offer model examples that could be profitably extended to other mountain systems whose small mammals are poorly known. The insufficiencies to be redressed for the mammalian fauna indigenous to Mesoamerican humid montane forests are essentially the same as those identified by Voss and Emons (1996:68–70) for Neotropical lowland rainforests.

(3) In addition to basic field inventory, the need for concerted systematic review of many montane forms, particularly those that are widely distributed, is sorely manifest. Many are species composites (see next discussion), and future revisions will necessarily alter the present snapshot of species diversity, geographic occurrence, and levels of endemism. Indeed, the dry environment of the Isthmus of Tehuantepec and its inhospitable nature for mesic-adapted organisms encourage the prediction that no species of small terrestrial mammal restricted to middle to upper montane humid forest has constituent populations distributed in mountains on both sides of it. This should be the operable null hypothesis requiring falsification as systematic revision of polytypic, widely distributed forms in Mesoamerica proceeds. The present tally of 76 species of shrews and small rodents thought to be restricted to Mesoamerican highland forest probably underestimates the biodiversity of these families by 30%, perhaps as much as 40%.

(4) Co-occurrence measures of faunal similarity and parsimony analyses of endemism, while useful exploratory approaches to highlight possible areas of endemism

and implicate zones of vicariance (e.g., see Harold & Mooi 1994), lack the power to critically invoke historical geographic events and their potential importance in the genesis of kinship patterns. The phenetic hierarchy among the montane regions divulged by resemblance coefficients is heavily influenced by the number of endemic species, counts of which speak little to their historical patterns of diversification. The structure of area relationships apparent from parsimony analyses of endemism stresses the coassociations of species presumed to be monophyletic. Unfortunately, these are precisely the same widely ranging, polytypic forms whose composite nature is most suspect. Nor can we presume that the heterogeneous elements of these nominal constructs, when eventually demonstrated to be specifically distinct, themselves form a monophyletic clade. Choate's (1970) definitions of *Cryptotis goldmani* and *C. mexicana* have been shown to be paraphyletic or polyphyletic mosaics in subsequent cladistic studies (Woodman & Timm 1999, 2000). The species segregated from *Peromyscus boylii* sensu Osgood (1909) or Hooper (1968) have proven to be members of at least two (Carleton 1989) or probably three (Tiemann-Boege et al. 2000) different species groups.

Well-supported hypotheses of phylogenetic relationship for multiple, co-occurring species provide a stronger basis for identification of concordant patterns of area relationship, and this is the great advantage supplied by the studies of Sullivan et al. (1997, 2000) and Woodman & Timm (1999). Many more small mammals distributed over the same Mesoamerican mountain ranges deserve comparable phylogenetic investigation and detailed systematic revision to assess the generality of the biogeographic patterns that their studies reveal.

Efforts to improve upon any one of these inadequacies, but especially points 2 and 3, will synergistically advance our understanding of the others.

Summary And Research Prospectus

The substantial genetic and morphological discontinuities now being uncovered within such broadly distributed species of Mesoamerican small mammals should surprise no one when the historical context of their definition is considered. Widespread ascension of the biological species concept, as taxonomically evidenced in the expanded usage of the trinomial, constrained the systematist's interpretation of interpopulational variation and its habitual nomenclatural expression, the subspecies. Operating under the guiding paradigm of the New Systematics, taxonomic revisions conducted throughout the early to middle 1900s served to accrete more or less distinctive forms as widely ranging, polytypic species, for example as neatly mapped in Hall (1981), and in doing so, superficially imparted a well understood foundation of species systematics and geographic distributions. With regard to biogeographic understanding of Mesoamerican small mammals, such protean specific constructs, ranging over highlands from southern Mexico to western Panama, obscured or diminished appreciation of potential barriers such as the Isthmus of Tehuantepec and the Nicaraguan Depression whenever systematists pondered the distributional limits of Neotropical species.

The improved investigational tools (morphometry, karyology, electrophoresis, gene sequencing) and methodological advancements (cladistics, phylogenetic species, vicariant biogeography, phylogeography), as they began to enter the practice of systematic mammalogy in the late 1900s, simply confer a more rigorous conceptual framework and improved analytic procedures to refine the systematic foundation handed down from the New Systematics era. Of relevance here, these fresh approaches to questions of species-level taxonomy provide explicit and concrete evaluation of variation, most notably as they bear on the kinds of evidence marshalled by our sys-

tematic predecessors to support population-intergradation, a conclusion integral to adducing conspecificity. For them, the criterion of intergradation, whether actually demonstrated (seldom) or plausibly inferred (often), was practically applied in two ways.

One involved the expectation that morphological intermediacy would be found to characterize geographically intermediate populations between two otherwise distinctive forms, whether separated by great or small distances. Thus, Osgood (1909:123–124), in justifying his subspecific arrangement of *Peromyscus leucopus*, reasoned that “If we suppose that *leucopus*, *texanus*, etc., have continuous distribution with gradual intergradation (and no doubt this is the case), we should expect to find specimens in central Oklahoma intermediate in character between *aridulus* and *texanus* on the one hand and between *leucopus* and *texanus* on the other.” Vouchered documentation of intergradation between these subspecies in Oklahoma was eventually confirmed, although Osgood could hardly have foreseen the fertile evolutionary essays on step clines, hybrid tension zones, and genetic introgression that his pragmatic classificatory outline would one day animate (Baker et al. 1983, Stangl & Baker 1984a, Stangl 1986, Nelson et al. 1987). In his study of variation and subspeciation within *Peromyscus truei*, Hoffmeister (1951:48) did recognize an abrupt shift in certain morphological features around the U.S.–Mexican boundary, but supposed that “the zone of intergradation between *truei* and *gentilis* [now = *P. gratus*] is narrow.” In this instance, finer regional sampling in southern New Mexico and recourse to discretely assortative traits such as chromosomal inversions and protein alleles have not sustained Hoffmeister’s conclusion (Zimmermann et al. 1978, Modi & Lee 1984, Janecek 1990); however, his treatment was certainly reasonable and understandable given the geographic samples then at hand, existing univariate methods for analyzing variation, and

period conventions for representing species-level taxonomic hypotheses.

The second evidentiary standard for intergradation involved the detection of morphological extremes within a homogeneous population, or geographically discrete set of populations, that purportedly overlapped or bridged the diagnostic traits cited for named geographic isolates. In arguing the synonymy of *Reithrodontomys sumichrasti* (in the highlands west of the Isthmus of Tehuantepec) and *dorsalis* (in highlands to the east), Hooper (1952:79) acknowledged that “it is improbable that their populations are continuous at the present time,” yet “There is now ample evidence of intergradation, through individual variation, of *dorsalis* and *sumichrasti*; they can best be treated as conspecific.” Whether viewed as a species (Howell 1914) or subspecies (Hooper 1952), each geographic grouping is strongly characterized morphologically, and as revealed by recent molecular research (Sullivan et al. 2000), highly distinctive genetically as well. In like manner, Musser (1969:17) judged the two “morphologically distinctive” but wholly “insular groups” of *Habromys* (*lepturus* and *ixtlani*) to “intergrade through individual variation,” a prediction not sustained by morphometric evaluation of that variation.

The new information sources, analytical techniques, and methodological rigor that emerged in the late 1900s will supply critical examination of either notion of intergradation, but they will prove crucially pivotal in reappraising interpretations of the second kind, the “individual variation” once used to conclude the specific synonymy of more or less distinctive geographic isolates. Polytypic candidates for renewed revisionary attention abound among Mesoamerica’s small terrestrial mammals distributed in highland settings: *Sorex saussurei*, *S. veraepacis*, *Cryptotis mexicana*, and *C. parva*; *Oryzomys chapmani*; *Peromyscus aztecus* and *P. baetae*; and *Reithrodontomys sumichrasti*, *R. fulvescens*, *R. mexicanus*, and *R. microdon*. Systematic

scrutiny should also be devoted to forms with extensive altitudinal ranges—e.g., species of *Liomys*, *Heteromys desmarestianus*, *Neotoma mexicana*, *Peromyscus mexicanus*, *Reithrodontomys fluvescens*, *R. megalotis*, *Sigmodon hispidus*—elements of which may also prove to be members of these highland assemblages. And of course, taxonomic review of broadly distributed lowland taxa and their differentiation along and across the eastern versus western versants of Mesoamerica are similarly warranted. The informed (!!!) dismantling of these species composites (see next) will divulge a clearer picture of mammalian biodiversity within the region, provide a firmer basis for identifying exemplars in phylogenetic studies, and encourage wider application of a well documented species taxonomy to issues of Mesoamerican biogeography equivalent to those already available for the herpetofauna and avifauna. Such goals comprise an integrated research venue as rich in potential evolutionary and biogeographic dividends as those that have unfolded from the lively systematic research on mammals in the mountains and basins of western North America (e.g., see Brown 1978; Hafner & Sullivan 1995; Riddle 1995, 1998).

In view of the substantial genetic divergences disclosed, the specific separation between populations of *Peromyscus aztecus* or *Reithrodontomys sumichrasti* to the west and east of the Tehuantepec corridor is probable. And, while one is tempted to hastily acknowledge each of these clades as species and to merely select the oldest available epithet within each region, such taxonomic changes should be firmly grounded within thoughtful systematic revisions, as Sullivan et al. (1997, 2000) have prudently recommended. The possibility, or rather the probability, exists for even greater taxonomic complexity hidden by the current classifications, since other name-bearing types have been designated for those southern populations of “*aztecus*” and “*sumichrasti*.” In both cases, the single

area designation “Nuclear Central America” overly simplifies a complex geomorphology and dynamic epicenter of historical geography within northern Mesoamerica, wherein the likelihood of population fragmentation and additional specific differentiation is strong. The continuing saga of *Peromyscus* “*boylii*,” a polytypic construction of the early to middle 1900s (Osgood 1909, Hooper 1968) from which an astonishing amount of species diversity has emerged over the past 25 years (see Carleton 1989 and Tiemann-Boege et al. 2000 for summaries), recommends a balanced approach that draws upon a variety of character data and that integrates geographic surveys designed to resolve specific taxonomic questions within and among the regions of interest.

Taxonomic Summary

Habromys Hooper & Musser

Peromyscus (*Habromys*) Hooper & Musser, 1964:12 (type species—*Peromyscus lepturus* Merriam, 1898).

Habromys: Carleton, 1980:125.—1989:122.

Habromys lepturus (Merriam, 1898)

Peromyscus lepturus Merriam, 1898:118 (type locality—México, Oaxaca, Mount Zempoaltepec, 8200 ft; holotype—USNM 68612).

Habromys lepturus: Carleton, 1989:122.

Distribution.—Narrow altitudinal zone (2500–3000 m) on the upper slopes of Cerro Zempoaltepec, northcentral Oaxaca, México.

Specimens examined.—México, *Estado Oaxaca*, Totontepec (USNM 68642); Mount Zempoaltepec, 8200 ft (AMNH 13892; USNM 68609, 68612–68615, 68618, 68619); northwest slope of Cerro Zempoaltepec, 3000 m (KU 124504–124506, 124511–124515, 124516–124531); southeast slope of Cerro Zempoaltepec, 3000 m (KU 124507, 124508).

Habromys ixtlani (Goodwin, 1964)

Peromyscus ixtlani Goodwin, 1964:3 (type locality—México, Oaxaca, District of Ixtlán, Cerro Machin, 5 km NE of Macuiltianguis, 9000 ft; holotype—AMNH 182099).

Peromyscus lepturus ixtlani: Musser, 1969: 17 (reassigned as subspecies).

Habromys lepturus [ixtlani]: Musser & Carleton, 1993:703 (cited in synonymy without indication of rank).

Distribution.—Upper gulf-facing and interior slopes of the Sierra de Juárez, north-central Oaxaca; documented altitudinal occurrence from 2350 to 3150 m.

Specimens examined.—México, *Estado Oaxaca*, Distrito Ixtlán, Cerro Machín, 5 km NE Macuiltianguis, 9000 ft (AMNH 182098, 182100–182104, 182133, 182143); 5.2 mi NNE (by rd) El Machin, 2600 m (MVZ 159722–159727, 159729, 161263–161273); 12 mi SSW Vista Hermosa, 9300 ft (KU 99990, 99991); 28.6 km S (by rd) Vista Hermosa, 2350 m (KU 124108, 124109, 124111–124118, 124492–124497, 124499–124501); 31 km S (by rd) Vista Hermosa (KU 136590); 31.6 km S (by rd) Vista Hermosa, north slope of Cerro Pelón, 2650 m (KU 124119, 124120, 124470–124491, 124637, 124470); northeast slope of Cerro Pelón, 2620 m (KU 120683–120686); Cerro Pelón, 9400 ft (UMMZ 114512–114515); Llano de Las Flores, 2800, 2900, and 3150 m (AMNH 212401; KU 92430, 120687, 121433–121437, 124121–124127, 124502); 12 mi N Ixtlán de Juárez, Llano de Las Flores, 9200 ft (UMMZ 109069–109074, 109639–109648); north of Llano de Las Flores, 9500 ft (UMMZ 112821–112835, 113085–113087); 11 mi NE (by Tuxtepec rd) Llano de Las Flores, 9100 ft (UMMZ 112836–112841); 13 mi NE (by Tuxtepec rd) Llano de Las Flores, southern slopes of Cerro Pelón, 9200 ft (112842–112864, 113084, 113788–113800); 4 mi SW (by rd) Llano de Las Flores, 8200 ft (UMMZ 112820).

Habromys lophurus (Osgood, 1904)

Peromyscus lophurus Osgood, 1904:72 (type locality—Guatemala, Huehuetenango, Todos Santos; holotype—USNM 77219).

Habromys lophurus: Carleton, 1989:122.

Distribution.—Middle to upper montane habitats (1950–3110 m) east and south of the Isthmus of Tehuantepec, from southern Chiapas, México, through central Guatemala, to northernmost El Salvador.

Specimens examined.—El Salvador, *Departamento Chalatenango*, Los Esesmiles, 8000 ft (MVZ 98615–98617, 131812). Guatemala, *Departamento Chimaltenango*, Tecpan, Chichavac, 8800 ft (FMNH 41744); *Departamento Huehuetenango*, 2 mi S San Juan Ixcoy, 9340 ft (KU 65495, 65497–65499, 65501, 65503, 65506, 65511); 4 km NW Santa Eulalia, “Yayquich,” 2950 m (UMMZ 118035–118049, 118363–118367); Todos Santos (USNM 77218–772122, 77224). *Departamento San Marcos*, southern slope of Volcán Tajumulco, 10,000 ft (UMMZ 99579). *Departamento Quezaltenango*, Calel, 10,200 ft (USNM 77261, 77262). MEXICO, *Estado Chiapas*, Pinabete (USNM 77618, 77631, 77632, 77637, 77638); Triunfo, 1950 m (UMMZ 88312–88316, 88318); San Cristóbal de Las Casas (USNM 75992–75994, 76600); Cerro Tzontehuitz, 3000 m (UMMZ 118050).

Habromys simulatus (Osgood, 1904)

Peromyscus simulatus Osgood, 1904:72 (type locality—México, Veracruz, near Jico, 6000 ft; holotype—USNM 55028).

Habromys simulatus: Carleton, 1989:122.

Distribution.—Currently known from widely scattered localities along the eastern slopes (1830–2200 m) of the Sierra Madre Oriental, from southern Hidalgo to northern Oaxaca, México.

Specimens examined.—México, *Estado Hidalgo*, Municipio Tenango de Doria, 10 km SW Tenango de Doria, El Potrero, 2200

m (BYU 15050); *Estado Oaxaca*, Distrito Teotitlan, 1.5 km S Puerto de la Soledad, 2200 m; 18° 09.742' N, 96° 59.852' W (BYU 15051–15053); *Estado Veracruz*, near Jico, 6000 ft (USNM 55027, 55028); 3 km W Zacualpan, 6000 ft (KU 83263).

Habromys chinanteco (Robertson & Musser, 1976)

Peromyscus chinanteco Robertson & Musser, 1976:1 (type locality—México, Oaxaca, northern slope of Cerro Pelón, 31.6 km S Vista Hermosa, 2650 m; holotype—KU 124130).

Habromys chinanteco: Carleton, 1989:122.

Distribution.—Gulf-facing slopes (2080–2650 m) of Cerro Pelón, Sierra de Juárez, in northcentral Oaxaca, México.

Specimens examined.—México, *Estado Oaxaca*, Distrito Ixtlán, 21 km S (by rd) Vista Hermosa, 2080 m (KU 136589); 28.6 km S (by rd) Vista Hermosa, 2350 m (KU 124129); 31.6 km S (by rd) Vista Hermosa, northern slope of Cerro Pelón, 2650 m (KU 124130, 124131, 124532); 16 mi SSW La Esperanza, 8000 ft (AMNH 254780).

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Appendix I.—Descriptive statistics for selected external and cranial variables and OTUs of *Habromys*.

Species and OTU	n	Mean	Range	SD
Total length				
<i>H. delicatulus</i> (OTU 6)	6	156	148–163	5
<i>H. chinanteco</i> (OTU 1)	5	199	192–212	9
<i>H. simulatus</i> (OTUs 12–13)	7	183	168–203	12
<i>H. ixtlani</i>				
(OTU 2)	43	249	210–273	14
(OTU 4)	57	249	221–280	13
<i>H. lepturus</i> (OTU 5)	24	233	207–262	11
<i>H. lophurus</i>				
(OTU 7)	11	208	187–220	11
(OTU 9)	12	211	195–230	12
Head and Body length				
<i>H. delicatulus</i> (OTU 6)	6	78	73–82	3
<i>H. chinanteco</i> (OTU 1)	5	90	87–92	2
<i>H. simulatus</i> (OTUs 12–13)	7	89	82–94	5
<i>H. ixtlani</i>				
(OTU 2)	43	117	100–130	7
(OTU 4)	57	123	105–145	8
<i>H. lepturus</i> (OTU 5)	24	113	94–125	7
<i>H. lophurus</i>				
(OTU 7)	11	99	84–108	7
(OTU 9)	12	101	92–110	6
Tail length				
<i>H. delicatulus</i> (OTU 6)	6	78	74–81	2
<i>H. chinanteco</i> (OTU 1)	5	109	103–121	8
<i>H. simulatus</i> (OTUs 12–13)	7	94	78–111	10
<i>H. ixtlani</i>				
(OTU 2)	43	132	110–147	9
(OTU 4)	57	126	100–147	10
<i>H. lepturus</i> (OTU 5)	24	120	103–146	9
<i>H. lophurus</i>				
(OTU 7)	11	109	92–115	7
(OTU 9)	12	110	99–125	8
Hindfoot length				
<i>H. delicatulus</i> (OTU 6)	6	19.2	18–20	0.7
<i>H. chinanteco</i> (OTU 1)	6	23.3	23–24	0.5
<i>H. simulatus</i> (OTUs 12–13)	7	22.6	21–24	1.0
<i>H. ixtlani</i>				
(OTU 2)	48	28.9	28–31	0.8
(OTU 4)	58	28.3	27–30	0.9
<i>H. lepturus</i> (OTU 5)	29	26.5	24–28	1.0
<i>H. lophurus</i>				
(OTU 7)	5	24.7	24–25	0.4
(OTU 9)	13	23.9	23–25	0.7
Ear length				
<i>H. delicatulus</i> (OTU 6)	6	19.4	18–20	0.7
<i>H. chinanteco</i> (OTU 1)	6	17.5	16–18	0.8
<i>H. simulatus</i> (OTUs 12–13)	5	17.8	16–19	1.3
<i>H. ixtlani</i>				
(OTU 2)	48	21.6	20–24	0.8
(OTU 4)	57	21.3	20–24	1.0
<i>H. lepturus</i> (OTU 5)	21	21.6	20–23	0.8
<i>H. lophurus</i> (OTU 9)	7	18.7	17–19	0.7

Appendix I.—Continued.

Species and OTU	n	Mean	Range	SD
Weight				
<i>H. delicatulus</i> (OTU 6)	6	13.5	10–19	3.1
<i>H. chinanteco</i> (OTU 1)	5	19.3	17–22	2.1
<i>H. simulatus</i> (OTUs 12–13)	5	17.8	17–19	0.8
<i>H. ixtlani</i>				
(OTU 2)	48	42.8	26–54	6.6
(OTU 4)	50	42.8	29–55	5.7
<i>H. lepturus</i> (OTU 5)	1	31.4		
<i>H. lophurus</i> (OTU 9)	7	32.4	24–41	5.7
Occipitonasal length				
<i>H. delicatulus</i> (OTU 6)	6	22.7	22.1–23.3	0.4
<i>H. chinanteco</i> (OTU 1)	6	26.0	25.6–26.5	0.2
<i>H. simulatus</i> (OTUs 12–13)	7	25.9	24.4–26.9	0.9
<i>H. ixtlani</i>				
(OTU 2)	46	30.8	27.5–32.6	1.0
(OTU 4)	60	30.9	28.8–32.9	0.7
<i>H. lepturus</i> (OTU 5)	27	29.7	28.1–30.8	0.7
<i>H. lophurus</i>				
(OTU 7)	10	27.1	25.4–28.1	0.9
(OTU 9)	13	27.5	25.6–28.5	0.9
Zygomatic breadth				
<i>H. delicatulus</i> (OTU 6)	6	11.7	11.4–12.2	0.3
<i>H. chinanteco</i> (OTU 1)	6	13.1	12.9–13.6	0.3
<i>H. simulatus</i> (OTUs 12–13)	7	13.2	12.4–13.5	0.4
<i>H. ixtlani</i>				
(OTU 2)	46	15.5	14.2–16.7	0.5
(OTU 4)	60	15.6	14.1–16.7	0.5
<i>H. lepturus</i> (OTU 5)	27	15.1	14.1–15.6	0.4
<i>H. lophurus</i>				
(OTU 7)	10	14.0	13.1–14.9	0.5
(OTU 9)	13	14.5	13.3–16.4	0.7
Breadth of zygomatic plate				
<i>H. delicatulus</i> (OTU 6)	6	1.6	1.5–1.7	0.06
<i>H. chinanteco</i> (OTU 1)	6	1.9	1.9–2.0	0.05
<i>H. simulatus</i> (OTUs 12–13)	7	2.0	1.8–2.2	0.12
<i>H. ixtlani</i>				
(OTU 2)	46	2.7	2.1–3.0	0.17
(OTU 4)	60	2.7	2.3–3.1	0.17
<i>H. lepturus</i> (OTU 5)	27	2.6	2.3–2.8	0.15
<i>H. lophurus</i>				
(OTU 7)	10	2.3	1.9–2.5	0.19
(OTU 9)	13	2.3	2.0–2.7	0.21
Interorbital breadth				
<i>H. delicatulus</i> (OTU 6)	6	4.0	3.9–4.1	0.1
<i>H. chinanteco</i> (OTU 1)	6	4.4	4.3–4.5	0.1
<i>H. simulatus</i> (OTUs 12–13)	7	4.4	4.3–4.5	0.1
<i>H. ixtlani</i>				
(OTU 2)	46	4.6	4.3–5.0	0.2
(OTU 4)	60	4.7	4.3–4.9	0.1
<i>H. lepturus</i> (OTU 5)	27	4.5	4.3–4.7	0.1
<i>H. lophurus</i>				
(OTU 7)	10	4.2	4.0–4.5	0.1
(OTU 9)	13	4.3	4.1–4.8	0.2

Appendix I.—Continued.

Species and OTU	n	Mean	Range	SD
Breadth of braincase				
<i>H. delicatulus</i> (OTU 6)	6	10.9	10.7–11.3	0.2
<i>H. chinanteco</i> (OTU 1)	5	12.1	12.0–12.3	0.1
<i>H. simulatus</i> (OTUs 12–13)	7	12.1	11.8–12.3	0.2
<i>H. ixtlani</i>				
(OTU 2)	46	12.7	12.1–13.2	0.2
(OTU 4)	60	12.7	12.2–13.1	0.2
<i>H. lepturus</i> (OTU 5)	27	12.5	11.9–13.5	0.3
<i>H. lophurus</i>				
(OTU 7)	10	11.8	11.0–12.6	0.5
(OTU 9)	13	12.1	11.6–12.5	0.3
Breadth across occipital condyles				
<i>H. delicatulus</i> (OTU 6)	6	5.4	5.3–5.5	0.1
<i>H. chinanteco</i> (OTU 1)	6	5.9	5.8–6.1	0.1
<i>H. simulatus</i> (OTUs 12–13)	7	5.9	5.7–6.1	0.2
<i>H. ixtlani</i>				
(OTU 2)	46	6.8	6.0–7.2	0.2
(OTU 4)	60	6.7	6.4–7.1	0.2
<i>H. lepturus</i> (OTU 5)	27	6.6	6.2–6.9	0.2
<i>H. lophurus</i>				
(OTU 7)	10	6.1	5.7–6.5	0.2
(OTU 9)	13	6.3	6.0–6.5	0.2
Height of braincase				
<i>H. delicatulus</i> (OTU 6)	6	8.5	8.4–8.7	0.1
<i>H. chinanteco</i> (OTU 1)	5	9.2	8.7–9.5	0.3
<i>H. simulatus</i> (OTUs 12–13)	7	9.3	8.9–9.9	0.4
<i>H. ixtlani</i>				
(OTU 2)	46	9.9	9.4–10.3	0.2
(OTU 4)	60	10.0	9.6–11.8	0.2
<i>H. lepturus</i> (OTU 5)	27	10.1	9.3–12.4	0.5
<i>H. lophurus</i>				
(OTU 7)	10	9.4	9.0–9.8	0.3
(OTU 9)	13	9.6	8.9–10.1	0.4
Length of rostrum				
<i>H. delicatulus</i> (OTU 6)	6	7.3	7.0–7.7	0.2
<i>H. chinanteco</i> (OTU 1)	6	8.9	8.5–9.4	0.3
<i>H. simulatus</i> (OTUs 12–13)	7	8.7	8.3–9.3	0.4
<i>H. ixtlani</i>				
(OTU 2)	46	11.3	9.8–12.2	0.5
(OTU 4)	60	11.1	9.8–12.1	0.4
<i>H. lepturus</i> (OTU 5)	27	10.4	9.6–11.1	0.4
<i>H. lophurus</i>				
(OTU 7)	10	9.0	8.5–9.3	0.2
(OTU 9)	13	9.3	8.2–9.8	0.5
Breadth of Rostrum				
<i>H. delicatulus</i> (OTU 6)	6	3.9	3.9–4.0	0.1
<i>H. chinanteco</i> (OTU 1)	6	4.6	4.3–4.8	0.2
<i>H. simulatus</i> (OTUs 12–13)	7	4.6	4.2–4.9	0.2
<i>H. ixtlani</i>				
(OTU 2)	46	5.2	4.8–5.7	0.2
(OTU 4)	60	5.2	4.6–5.9	0.3

Appendix I.—Continued.

Species and OTU	n	Mean	Range	SD
<i>H. lepturus</i> (OTU 5)	27	5.1	4.6–5.7	0.2
<i>H. lophurus</i>				
(OTU 7)	10	4.5	4.1–4.8	0.3
(OTU 9)	13	4.7	4.3–5.1	0.2
Length of diastema				
<i>H. delicatulus</i> (OTU 6)	6	5.7	5.5–5.9	0.2
<i>H. chinanteco</i> (OTU 1)	6	6.5	6.2–6.8	0.3
<i>H. simulatus</i> (OTUs 12–13)	7	6.6	6.1–6.9	0.3
<i>H. ixtlani</i>				
(OTU 2)	46	8.2	7.1–9.0	0.4
(OTU 4)	60	8.3	7.4–8.9	0.3
<i>H. lepturus</i> (OTU 5)	27	7.6	6.9–8.1	0.3
<i>H. lophurus</i>				
(OTU 7)	10	6.7	6.3–7.2	0.3
(OTU 9)	13	6.9	5.9–7.3	0.4
Length of incisive foramen				
<i>H. delicatulus</i> (OTU 6)	6	4.6	4.4–4.7	0.1
<i>H. chinanteco</i> (OTU 1)	6	5.0	4.7–5.2	0.2
<i>H. simulatus</i> (OTUs 12–13)	7	5.2	4.9–5.5	0.3
<i>H. ixtlani</i>				
(OTU 2)	46	6.3	5.3–7.1	0.3
(OTU 4)	60	6.5	6.0–7.1	0.2
<i>H. lepturus</i> (OTU 5)	27	6.1	5.6–6.6	0.2
<i>H. lophurus</i>				
(OTU 7)	10	5.8	5.5–6.2	0.2
(OTU 9)	13	5.6	5.1–6.0	0.3
Breadth of incisive foramina				
<i>H. delicatulus</i> (OTU 6)	6	1.6	1.5–1.7	0.06
<i>H. chinanteco</i> (OTU 1)	6	2.0	1.9–2.1	0.08
<i>H. simulatus</i> (OTUs 12–13)	7	1.9	1.7–2.0	0.10
<i>H. ixtlani</i>				
(OTU 2)	46	2.2	1.9–2.5	0.13
(OTU 4)	60	2.2	1.9–2.5	0.11
<i>H. lepturus</i> (OTU 5)	27	2.2	2.0–2.4	0.13
<i>H. lophurus</i>				
(OTU 7)	10	1.9	1.8–2.1	0.09
(OTU 9)	13	2.0	1.8–2.2	0.14
Length of bony palate				
<i>H. delicatulus</i> (OTU 6)	6	3.4	3.3–3.5	0.1
<i>H. chinanteco</i> (OTU 1)	6	4.3	3.9–4.5	0.2
<i>H. simulatus</i> (OTUs 12–13)	7	3.8	3.6–4.3	0.2
<i>H. ixtlani</i>				
(OTU 2)	46	5.1	4.5–5.6	0.3
(OTU 4)	60	5.0	4.6–5.5	0.2
<i>H. lepturus</i> (OTU 5)	27	4.4	4.1–4.8	0.2
<i>H. lophurus</i>				
(OTU 7)	10	4.1	3.9–4.4	0.1
(OTU 9)	13	4.1	3.5–4.4	0.2
Palatal breadth between M1s				
<i>H. delicatulus</i> (OTU 6)	6	2.5	2.4–2.6	0.1
<i>H. chinanteco</i> (OTU 1)	6	2.7	2.6–2.9	0.1
<i>H. simulatus</i> (OTUs 12–13)	7	2.8	2.7–3.1	0.1

Appendix I.—Continued.

Species and OTU	n	Mean	Range	SD
<i>H. ixtlani</i>				
(OTU 2)	46	3.1	2.8–3.4	0.1
(OTU 4)	60	3.1	2.7–3.7	0.2
<i>H. lepturus</i> (OTU 5)	27	3.0	2.5–3.4	0.2
<i>H. lophurus</i>				
(OTU 7)	10	2.5	2.2–2.8	0.2
(OTU 9)	13	2.7	2.4–3.1	0.2
Width of mesopterygoid fossa				
<i>H. delicatulus</i> (OTU 6)	6	1.5	1.4–1.6	0.07
<i>H. chinanteco</i> (OTU 1)	6	1.8	1.6–1.8	0.08
<i>H. simulatus</i> (OTUs 12–13)	7	1.7	1.6–1.8	0.08
<i>H. ixtlani</i>				
(OTU 2)	46	2.1	1.8–2.4	0.17
(OTU 4)	60	2.1	1.7–2.4	0.16
<i>H. lepturus</i> (OTU 5)	27	1.9	1.8–2.1	0.09
<i>H. lophurus</i>				
(OTU 7)	10	1.8	1.7–2.0	0.10
(OTU 9)	13	2.0	1.7–2.2	0.15
Postpalatal length				
<i>H. delicatulus</i> (OTU 6)	6	8.0	7.8–8.3	0.2
<i>H. chinanteco</i> (OTU 1)	6	8.9	8.6–9.1	0.2
<i>H. simulatus</i> (OTUs 12–13)	7	9.0	8.4–9.4	0.3
<i>H. ixtlani</i>				
(OTU 2)	46	10.9	9.1–11.7	0.5
(OTU 4)	60	11.0	10.1–11.8	0.3
<i>H. lepturus</i> (OTU 5)	27	10.4	9.6–11.0	0.3
<i>H. lophurus</i>				
(OTU 7)	10	9.5	8.9–10.0	0.4
(OTU 9)	13	9.7	9.1–10.2	0.3
Coronal length of maxillary toothrow				
<i>H. delicatulus</i> (OTU 6)	6	3.34	3.24–3.46	0.08
<i>H. chinanteco</i> (OTU 1)	6	3.89	3.81–4.01	0.07
<i>H. simulatus</i> (OTUs 12–13)	7	3.98	3.82–4.11	0.09
<i>H. ixtlani</i>				
(OTU 2)	49	5.17	4.88–5.45	0.14
(OTU 4)	60	5.08	4.72–5.45	0.16
<i>H. lepturus</i> (OTU 5)	27	4.92	4.69–5.12	0.12
<i>H. lophurus</i>				
(OTU 7)	10	4.71	4.42–4.83	0.12
(OTU 9)	13	4.58	4.44–4.68	0.11
Width of first upper molar				
<i>H. delicatulus</i> (OTU 6)	6	0.95	0.89–1.01	0.05
<i>H. chinanteco</i> (OTU 1)	6	1.09	1.06–1.13	0.02
<i>H. simulatus</i> (OTUs 12–13)	7	1.12	1.06–1.12	0.04
<i>H. ixtlani</i>				
(OTU 2)	49	1.46	1.38–1.55	0.03
(OTU 4)	60	1.43	1.33–1.53	0.05
<i>H. lepturus</i> (OTU 5)	27	1.37	1.25–1.44	0.05
<i>H. lophurus</i>				
(OTU 7)	10	1.27	1.23–1.33	0.03
(OTU 9)	13	1.31	1.25–1.38	0.05

Appendix I.—Continued.

Species and OTU	n	Mean	Range	SD
Breadth across upper incisor tips				
<i>H. delicatulus</i> (OTU 6)	6	1.28	1.20–1.40	0.07
<i>H. chinanteco</i> (OTU 1)	6	1.35	1.30–1.40	0.05
<i>H. simulatus</i> (OTUs 12–13)	7	1.35	1.30–1.40	0.04
<i>H. ixtlani</i>				
(OTU 2)	45	1.84	1.60–2.00	0.11
(OTU 4)	58	1.83	1.60–2.00	0.11
<i>H. lepturus</i> (OTU 5)	27	1.83	1.50–2.00	0.12
<i>H. lophurus</i>				
(OTU 7)	10	1.55	1.40–1.70	0.11
(OTU 9)	13	1.61	1.30–1.80	0.13