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A New Genus for *Aepeomys fuscatus* Allen, 1912, and *Oryzomys intectus* Thomas, 1921: Enigmatic Murid Rodents from Andean Cloud Forests

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ABSTRACT

Two nominal species of Neotropical murid rodents (subfamily Sigmodontinae) that have long been referred to different genera are here placed in a new genus in recognition of their distinctness from other named supraspecific taxa. *Aepeomys fuscatus* Allen and *Oryzomys intectus* Thomas share a unique combination of external and craniodental character states that diagnose *Handleyomys*, new genus, with *fuscatus* as its type species. Morphological comparisons of *Handleyomys* with the type species of *Aepeomys* Thomas and *Oryzomys* Baird provide a basis for preliminary inferences about phylogenetic relationships. Five shared, derived character states support the hypothesis that *Handleyomys* is an oryzomyine, but no close relationship between the new genus and any particular oryzomyine clade is indicated by the data at hand. All known specimens of *Handleyomys* are from the western Andes (Cordillera Occidental) and the central Andes (Cordillera Central) of Colombia, where they have been collected at 20 localities ranging in elevation from 1500 to 2800 m above sea level. Analyses of morphological data suggest that two valid allopatric species are represented, of which *H. fuscatus* is endemic to the western Andes and *H. intectus* to the central Andes. Although no other mammalian clade is known to have the same geographic distribution, recent analyses of amphibian biogeography in Colombia suggest that *Handleyomys* is part of a nonvolant cloud-forest vertebrate fauna with allopatric sister taxa in the Cordillera Occidental and Cordillera Central. Much revisionary taxonomic research, however, is needed to assess the generality of this pattern of endemism among other cloud-forest mammals.

RESUMEN

Dos especies nominales de roedores múridos neotropicales (subfamilia Sigmodontinae) que habían sido ubicadas durante mucho tiempo en géneros diferentes, se asignan a un nuevo género reconociendo sus diferencias con otros taxones nominales supraespecíficos. *Aepeomys fuscatus* Allen y *Oryzomys intectus* Thomas comparten una combinación única de estados de caracteres externos y craneodentales, que permiten diagnosticar a *Handleyomys* como un género nuevo, con *fuscatus* como su especie típica. Las comparaciones morfológicas entre *Handleyomys* y las especies típicas de los géneros *Aepeomys* Thomas y *Oryzomys* Baird proveen una base para hacer deducciones preliminares sobre sus relaciones filogenéticas. La hipótesis de que *Handleyomys* es un orizomino está apoyada por cinco estados de caracteres compartidos derivados, pero los datos disponibles no indican una relación estrecha entre el nuevo género y ningún clado particular de orizomino. Todos los espécimenes conocidos de *Handleyomys* provienen de las Cordilleras Occidental y Central de los Andes de Colombia, donde fueron recolectados en 20 localidades en alturas comprendidas entre 1500 y 2800 m sobre el nivel del mar. El análisis de los datos morfológicos sugiere la presencia de dos especies alopátricas válidas, de las cuales *H. fuscatus* es endémica de la Cordillera Occidental y *H. intectus* de la Cordillera Central. Aunque no se conoce ningún otro clado de mamíferos con una distribución geográfica similar, análisis biogeográficos recientes de anfibios de Colombia sugieren que *Handleyomys* forma parte de una fauna vertebrada no voladora de los bosques de niebla, con taxones alopátricos hermanos en la Cordillera Occidental y en la Cordillera Central. Para evaluar la generalidad de este patrón de endemismo entre otros mamíferos de los bosques nublados se requiere de mayores investigaciones taxonómicas.

INTRODUCTION

Extending from the Serranía de Perijá west of Lake Maracaibo southward to the yungas of central Bolivia is the largest region of tropical montane rain forest in the world. Isolated from similar habitats in Central America by the Río Atrato lowlands of northwestern Colombia, and from temperate mon-

tane rain forests in the southern Andes by treeless alpine deserts and grasslands, the cloud forests of the northern and central Andes harbor taxonomically distinctive mammalian communities that are among the least known of all terrestrial vertebrate faunas. Although a few large species are relatively well known as focal taxa for international conservation efforts—woolly tapirs (*Tapirus pin-*

chaque), spectacled bears (*Tremarctos ornatus*), pudus (*Pudu mephistopheles*), and yellow-tailed woolly monkeys (*Lagothrix flavicauda*)—the overwhelming majority of Andean cloud-forest mammals are small and virtually unstudied. Indeed, most museum collections of mammals from Andean cloud forests remain incompletely or inaccurately identified, with the result that patterns of species richness and endemism in this fauna are effectively unknown.

This report contributes to the analysis of mammalian diversity in the Andean cloud-forest biota by diagnosing a previously unrecognized clade of murid rodents from the western and central cordilleras of Colombia. Two species, both described early in the 20th century and long referred to different genera, are here placed in a new genus because of their uniquely shared combination of morphological characters. By doing so, we simplify the taxonomic context for two major phylogenetic studies currently in progress, and we draw attention to a distinctive lineage whose restricted ecogeographic distribution provides evidence for patterns of endemism that may be shared with other cloud-forest organisms.

MATERIALS AND METHODS

The material we examined consists of standard skin-and-skull preparations or fluid-preserved specimens deposited in the following institutional collections: AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (formerly the British Museum of Natural History, London); FMNH, Field Museum of Natural History (Chicago); ICN, Museo de Historia Natural del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (Bogotá); IND-M, Instituto Alexander von Humboldt (formerly INDERENA, Villa de Leiva); MBUCV, Museo de Biología, Universidad Central de Venezuela (Caracas); MLS, Museo del Instituto La Salle (Bogotá); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History (Washington, D.C.).

We transcribed total length (TL) and length of tail (LT) from specimen tags and

computed head-and-body length (HBL) by subtracting LT from TL. Length of the hind foot (HF, including claws) and of the external ear (Ear, from notch to distalmost margin of the pinna) were also transcribed from specimen tags; however, we usually remeasured hindfoot length on dried skins to check the accuracy of values recorded by the collector, and we used our values whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm).

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm. The following were measured as illustrated and defined by Voss (1988, 1991): CIL, condylo-incisive length; LD, length of diastema; LM, occlusal length of the maxillary molar row; BM1, breadth of the first maxillary molar; LIF, length of one incisive foramen; BIF, breadth across both incisive foramina; BPB, breadth of the palatal bridge (between the M1 protocones); BZP, breadth of the zygomatic plate; LIB, least interorbital breadth; ZB, zygomatic breadth. In addition, we measured nasal length (NL) as the greatest longitudinal dimension of either the right or left nasal bone, and interparietal breadth (IPB) as the greatest transverse dimension of the interparietal bone.

Except as noted below, all analyzed character data were obtained from nonsenescent adults as determined by dental and pelage criteria. A specimen was judged to be adult if the molar dentition was fully erupted (with M3 exhibiting at least some wear) and if the pelage was mature; old adults (with molars worn below the widest part of the crown) were not measured or scored for qualitative characters. In effect, the specimens used for our statistical analyses approximately correspond to toothwear classes 2–4 as defined by Voss (1991).

Qualitative character variation is described herein using anatomical terminology that is explained or referenced by Reig (1977), Voss (1988), Carleton and Musser (1989), Voss (1993), Voss and Carleton (1993), and Stepan (1995).

SYSTEMATICS

TAXONOMIC HISTORY

The first species treated in this report was originally described as *Aepeomys fuscatus* by Allen (1912) on the basis of 12 specimens collected by W. B. Richardson near the village of San Antonio in the western Andes of Colombia. An ornithologist by training, Allen focused his description on pelage texture, pigmentation, and other features of the preserved skins he examined, while ignoring all qualitative craniodental characters (p. 89):

Pelage long, thick, soft and velvety. Upperparts blackish, almost clear black over the median dorsal region, with a faint wash of grayish brown over the shoulders and on the sides of the body, almost imperceptible except in favorable lights, when the extreme tips of the hairs are seen to be grayish bistre; underparts dark gray, the pelage being slaty with the extreme tips of the hairs lighter or pale drab-gray; ears brown, thickly clothed with soft black hairs on the basal third externally, the rest nearly naked on both surfaces; feet flesh color, very thinly haired; tail light gray brown, nearly unicolor, naked.

From this description and accompanying measurements, all that a reader can infer was that Allen's new species was a small, soft-furred, dark-colored mouse with a naked tail approximately the same length as its head and body. Unfortunately, these traits are shared by many species of cloud-forest murids, few of which can be reliably distinguished by the additional details that Allen provided. The omission of qualitative craniodental character information, already widely recognized as important for muroid rodent systematics (e.g., by Thomas, 1906; Osgood, 1909; Goldman, 1910), was particularly unfortunate. In justifying his generic assignment, Allen (1912: 89) stated only that *fuscatus* "... is evidently related to *Aepeomys vulcani* Thomas, from which it appears to differ in relatively longer tail and somewhat in coloration."

The genus *Aepeomys* was originally named by Thomas (1898) to contain two taxa, of which the designated type species was *A. lugens* (Thomas, 1896) from Venezuela. Because the second referred taxon, *A. vulcani* Thomas (1898), was based on a specimen from Ecuador, the known range of *Aepeomys* (sensu Thomas) bracketed the type locality of *fuscatus*, and Allen's (1912) ge-

neric assignment at least made biogeographic sense. However, with all of the known material of *fuscatus* in New York, and the types of *lugens* and *vulcani* in London, no other taxonomic assessment was possible given the incompleteness of Allen's description.

Although *Aepeomys* was recognized as a valid genus by Gyldenstolpe (1932) and Tate (1932b), Osgood (1933) argued that the type species (*lugens*) was insufficiently divergent from the many forms then referred to *Thomasomys* Coues, 1884, to maintain this usage and concluded that *Aepeomys* was just a junior synonym. Osgood's judgment was subsequently endorsed by Ellerman (1941), who recognized *Thomasomys fuscatus*, *T. lugens*, and *T. vulcani* as valid species in his influential monograph on rodent classification. Cabrera (1961) likewise followed Osgood's inclusive sense of *Thomasomys*, but treated all of the taxa formerly referred to *Aepeomys* as conspecific, listing *fuscatus* and *vulcani* as subspecies of *T. lugens*.

Apparently, neither Osgood, Ellerman, nor Cabrera actually examined specimens of *fuscatus*, and no new character information about this taxon was subsequently published until Gardner and Patton's (1976) review of karyotypic variation among Neotropical murids. In that report, the authors analyzed chromosomal preparations from *fuscatus* and six other species of *Thomasomys* (sensu Osgood) and remarked that Allen's form was highly distinctive. They summarized their conclusions in the context of suprageneric (tribal-level) assemblages as then understood by taxonomists (p. 32):

The thomatomyine group ... includes *Thomasomys*, *Rhipidomys*, *Nyctomys*, *Otonyctomys*, and *Phaenomys*. Members of this group represented by our material ... include *Rhipidomys latimanus* and at least six species of *Thomasomys* (sensu lato). *Aepeomys* (= *Thomasomys*) *fuscatus* ($2n = 54$, $FN = 62$) is karyotypically the most aberrant representative and actually may not belong in the *Rhipidomys* and *Thomasomys* complex. Therefore, we are using the generic name *Aepeomys* for this form. Chromosomally it falls within the first oryzomyine group as exemplified by *Oryzomys palustris*, a group sharing chromosomal characters with various other groups ...

Most late 20th-century checklists (e.g., Honacki et al., 1982; Alberico, 1983; Cuervo-Díaz et al., 1986; Musser and Carleton, 1993; Alberico et al., 2000) have followed Gardner

and Patton (1976) in ranking *Aepeomys* as a valid genus, but the implicit hypothesis that its member species (*fuscatus*, *lugens*, and *vulcani*) form a natural (monophyletic) group remains effectively untested by any morphological, karyotypic, or biochemical data.

The second species treated in this report was originally described as *Oryzomys intectus* by Thomas (1921) on the basis of three specimens collected by Nicéforo María near Santa Elena in the central Andes of Colombia. Unlike Allen's description of *fuscatus*, Thomas's description of *intectus* included several relevant details of craniodental morphology (p. 356):

Skull peculiarly short, broad, and rounded, with broad interorbital region. Indeed, it is almost precisely like that of a *Melanomys*, with the important exception that there is no trace of the supraorbital beading so conspicuous in that group. Brain-case similarly low, smooth, and without ridges. Palatal foramina short, about the length of the tooth-row. Molars stout and heavy, large for the size of the animal, their structure more like that in *Melanomys* than in the smaller species of *Oryzomys*, but many of the larger species of *Oryzomys* also have quite similar molars.

From these and other comparisons, Thomas concluded that (p. 357):

This is a remarkably distinct species, whose systematic position is not at present easy to determine. Its peculiarly broad low skull distinguishes it from any *Oryzomys* known to me, while the entire absence of supraorbital ridges separates it from *Melanomys*, to which its short tail and the general shape of the skull perhaps indicate some affinity. Many *Oryzomys*, however, have no supraorbital ridges, and I therefore provisionally place it in that genus.

As the heterogeneous contents of *Oryzomys* were gradually sorted into species groups and subgenera by later generations of mammalogists, *intectus* remained an enigma, left unallocated by some authors (Ellerman, 1941) or referred to the nominate subgenus by default (Tate, 1932a; Cabrera, 1961). Despite recent advances in oryzomyine systematics that have resulted in several former subgenera of *Oryzomys* being elevated to generic rank (e.g., *Microryzomys*, *Oligoryzomys*, *Oecomys*; see Carleton and Musser [1989], Musser and Carleton [1993]), the classification of *intectus* has not been addressed by any published analysis or discussion of character data.

The chronology of the present study dates

from the 1970s, when the late Charles O. Handley, Jr. (then curator of mammals at the National Museum of Natural History) and RSV (then a graduate student at the University of Michigan) independently examined the type series of *Aepeomys fuscatus* and concluded that it had been misclassified by Allen (1912) and by all subsequent compilers of Neotropical murid checklists. Whereas *A. lugens* (the type species of *Aepeomys*) was clearly allied with *Thomasomys* and certain other "thomasomyines", *fuscatus* exhibited equally unambiguous similarities to oryzomyines. Rather than belonging to *Oryzomys* or other allied genera, however, *fuscatus* seemed to be a highly divergent form. Handley and RSV compared notes and agreed to collaborate on a joint report, but other projects intervened and only a few colleagues were informed about their results. In the meantime, Guy G. Musser examined the type series of *Oryzomys intectus* in London, recognized that it represented the same clade discovered by Handley and RSV, and generously provided them with copies of his notes; RSV followed this up by examining *intectus* himself on a subsequent visit to the Natural History Museum.

Other independent discoveries of essentially the same facts about *fuscatus* and *intectus* were made by MGL and VP; their results were based on new specimens and/or new characters (not previously considered by Handley and RSV), resulting in this collaboration. With the recent death of Charles Handley, it seems appropriate to name the new genus for him in recognition of his past participation in our work and in tribute to his many important contributions over the course of a long and productive career in Neotropical mammalogy (fig. 1).

Handleyomys, new genus

Figures 2–11

TYPE SPECIES: *Aepeomys fuscatus* Allen, 1912.

GEOGRAPHIC DISTRIBUTION: Known from the western and central Andean cordilleras of Colombia at elevations from ca. 1500 to 2800 m above sea level (fig. 12).

CONTENTS: Two species as redescribed below.



Fig. 1. Charles O. Handley, Jr. (right) with Carl Johnson (Director of the Gorgas Memorial Laboratory, left) at their camp on the Río Tacarcuna, Provincia Darién, Panama, in 1964. Photograph courtesy of the Smithsonian Institution Archives (Alexander Wetmore Papers, box 188: photograph 8793).

MORPHOLOGICAL DIAGNOSIS AND DESCRIPTION: Adult body pelage fine and soft, uniformly dull brownish-gray dorsally, usually darker (sometimes almost blackish) middorsally than on flanks; ventral pelage dark gray frosted with paler gray or buff, not sharply countershaded. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present; mystacial hairs neither very short nor very long, extending posteriorly to (but not beyond) caudal margins of pinnae when laid back against cheeks of properly made-up skins. Pinnae not large but clearly visible above fur of head, sparsely covered with short dark hairs. Manus sparsely covered dorsally with short pale (whitish or silvery) hairs; ventral surface naked and unpigmented, with five separate plantar tubercles

(two carpal and three interdigital pads); claws short, neither conspicuously elongated nor unusually recurved. Pes long and narrow, with outer digits (I and V) much shorter than middle three (claw of dI extending to middle of first phalange of dII, claw of dV extending just beyond first interphalangeal joint of dIV); conspicuous ungual tufts of long silvery hairs rooted at bases of claws on dII–dV, but pedal dorsum otherwise only sparsely covered with short pale or dark-banded hairs; plantar surface (including heel) naked, weakly pigmented (grayish in life), with two metatarsal and four interdigital pads; indistinct squamae (scale-like tubercles) sparsely distributed along outer distal plantar surfaces, but not in center of sole. Tail about as long as combined length of head and body,



Fig. 2. **Above:** *Handleyomys fuscatus* (ICN 12825) from El Campamento, Municipio Santuario, Departamento Risaralda (appendix: locality 14). **Below:** Pastures and disturbed primary cloud forest at about 2500 m elevation near El Campamento; specimens of *H. fuscatus* and six other species of murid rodents were captured in the forest at this locality (see text). Both photographs were taken by Marcela Morales during the rainy season (November) of 1991.

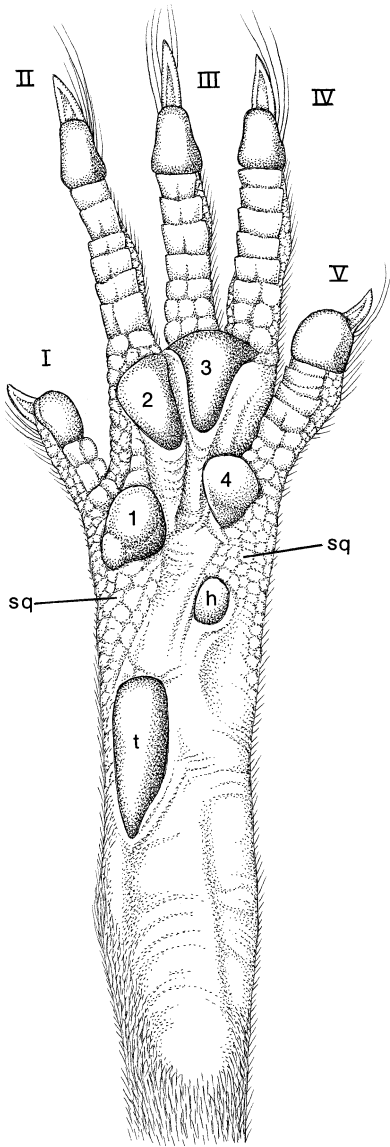


Fig. 3. Plantar view of left hind foot of *Han-dleyomys intectus* (ICN 16092). Distinctive characteristics of the genus include the narrow, hairless sole; six small plantar pads including thenar (t), hypothenar (h), and four interdigital (1–4) tubercles; very short hallux (I); long and subequal second (II), third (III), and fourth (IV) digits; short and non-opposable fifth digit (V); indistinct plantar squamae (sq); and unguis tufts of long hairs rooted at the bases of the claws of digits II–V.

apparently naked (a sparse caudal pelage is only visible under magnification), and unicolorous (dark above and below). Mammary six in inguinal, abdominal, and postaxial pairs.

Skull with long, tapering rostrum flanked by shallow but distinct zygomatic notches; interorbital region hourglass-shaped, neither greatly inflated nor unusually constricted, with rounded supraorbital margins; braincase moderately inflated and rounded, without prominent temporal crests, ridges, or beads. Zygomatic plate (in lateral view) moderately broad, its anterior edge vertical or nearly so (not sloping backward), with a rounded (never angular or spinous) anterodorsal contour. Premaxillae short (not produced anteriorly beyond incisors to form a rostral tube with nasals). Incisive foramina neither very short nor greatly elongated, averaging about 60% of diastemal length (not extending posteriorly between molar rows) and widest near premaxillary/maxillary sutures. Palatal bridge wide and long, without median ridge or deep lateral gutters; posterolateral pits usually large and often complex, typically consisting of two or more foramina recessed in a common fossa on each side. Mesopterygoid fossa not penetrating anteriorly between molar rows; bony roof of fossa complete or perforated only by narrow slits, never conspicuously fenestrated. Alisphenoid strut absent (buccinator-masticatory foramen and foramen ovale confluent). Carotid arterial morphology primitive, with orbitofacial circulation supplied by separate supraorbital and infraorbital branches of large stapedia artery (= pattern 1 of Voss, 1988); course of supraorbital stapedia ramus marked by prominent squamosal-alisphenoid groove and sphenofrontal foramen. Postglenoid foramen separated from large subsquamosal fenestra by slender hamular process of squamosal. Tegmen tympani not overlapping squamosal, or tegmen tympani-squamosal overlap weak (not involving a distinct posterior suspensory process of the latter bone). Bullae small; pars flaccida of tympanic membrane present, large; orbicular apophysis of malleus well developed.

Mandible with well-developed falciform coronoid process; lower incisor alveolus without distinct capsular process on lateral

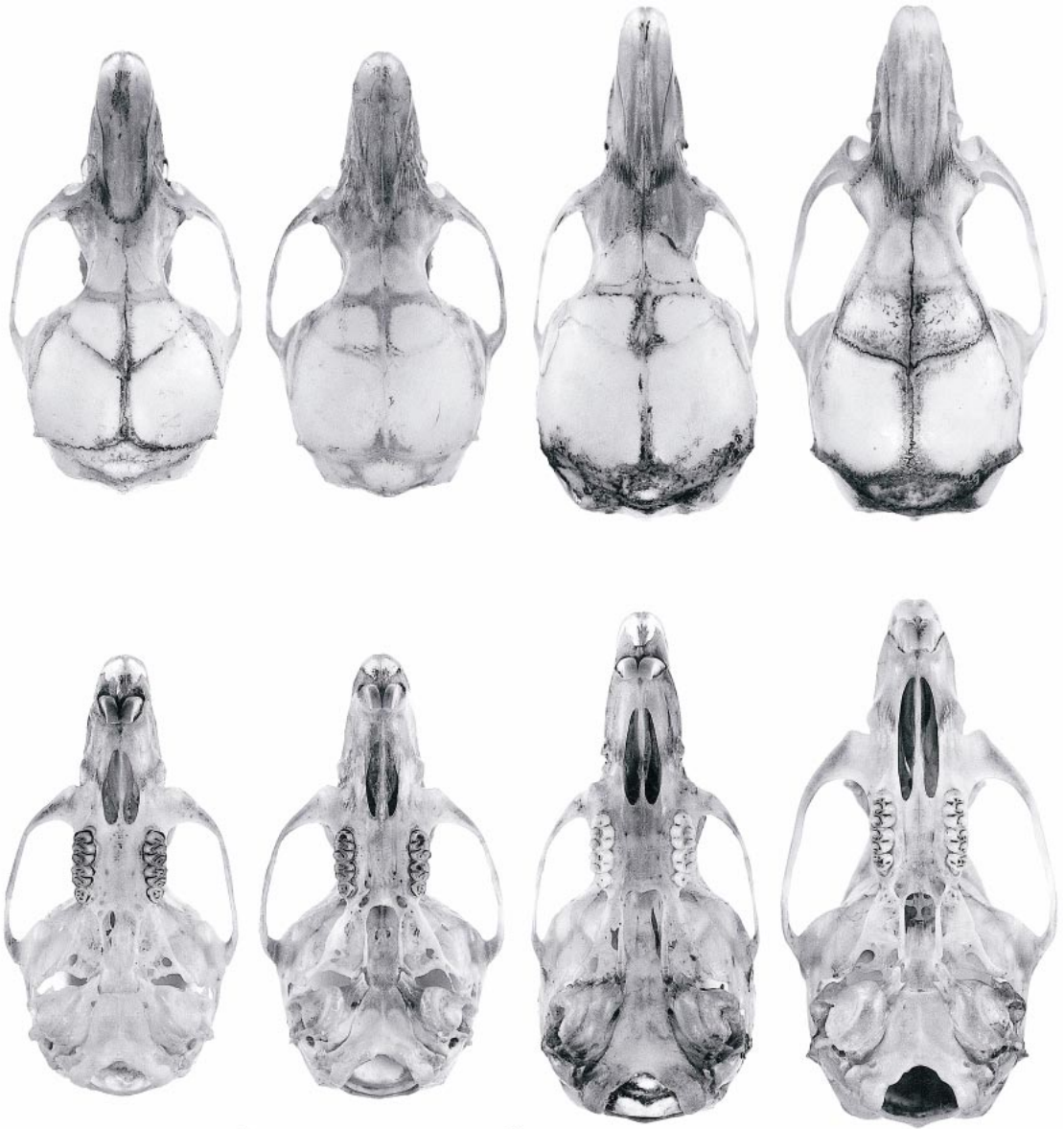


Fig. 4. Dorsal and ventral cranial views (ca. $\times 2$) of *Handleyomys*, *Aepeomys* and *Oryzomys*. From left to right: *H. fuscatus* (ICN 12703), *H. intactus* (ICN 16092), *A. lugens* (AMNH 143670), *O. palustris* (AMNH 242524).

mandibular surface. Basihyal morphology unknown.

Incisors ungrooved, with yellow-orange enamel bands; upper teeth small, narrow, deeper than wide, opisthodont; lower teeth unremarkable in coloration or morphology.

Maxillary molar rows parallel; principal cusps arranged in opposite labial/lingual

pairs, bunodont when unworn but quickly eroded with age to same level as other enamelled structures (occlusal surface of most adult teeth more-or-less planar); labial and lingual reentrant folds long and interpenetrating (incipiently lophodont sensu Voss, 1993); M1 anterocone entire, not divided into labial and lingual conules (anteromedian

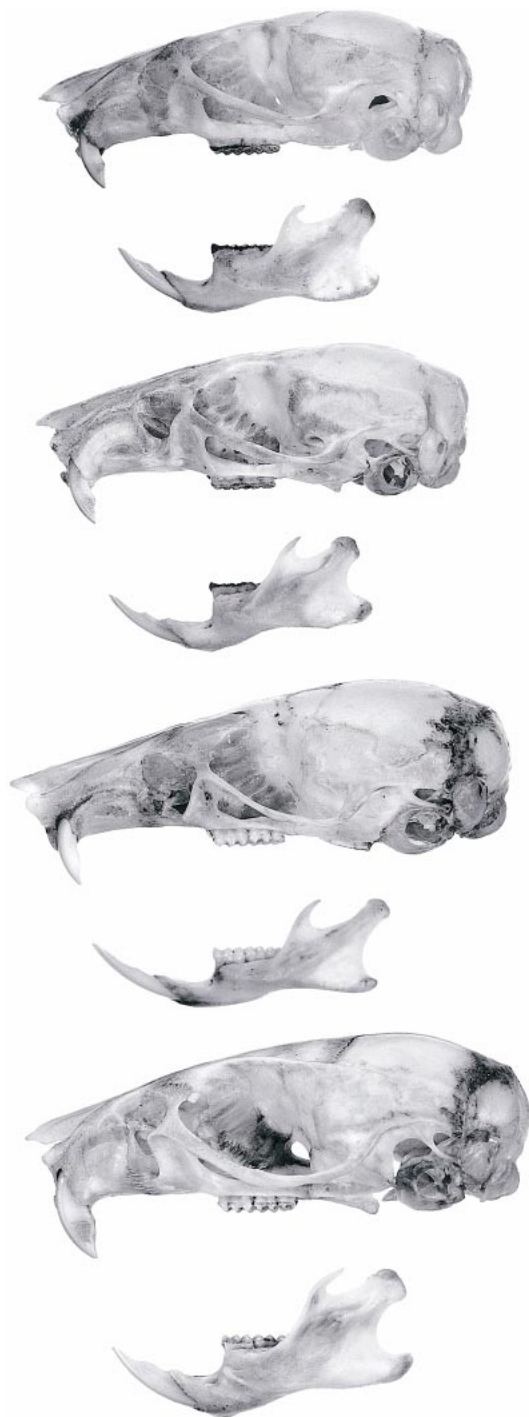


Fig. 5. Lateral cranial and mandibular views (ca. $\times 2$) of *Handleyomys*, *Aepeomys*, and *Oryzomys*. From top to bottom: *H. fuscatus* (ICN 12703), *H. intectus* (ICN 16092), *A. lugens* (AMNH 143670), *O. palustris* (AMNH 242524).

flexus absent); anteroflexus very deep, extending lingually beyond dental midline on M1 and M2; anterolophs and mesolophs large, fused with corresponding (antero- and meso-) styles on labial margins of M1 and M2; posterolophs distinct on M1 and M2, persisting with moderate to heavy wear; M3 subtriangular, smaller than more anterior teeth, with most of the same occlusal elements but usually without distinct hypocone or posteroloph. First maxillary molar with one accessory labial root (four roots total); M2 and M3 three-rooted.

Anteroconid of first mandibular molar (m1) undivided by median flexid, fused with protolophid and/or anterolophid to enclose a persistent internal fold of uncertain homology (anteroflexid and/or protoflexid); anterolophid absent on m2 and m3; anterolabial cingulum absent or indistinct on m2, consistently absent on m3; mesolophids and posterolophids large and well developed on all mandibular teeth; ectolophids consistently absent. First mandibular molar with an accessory labial root, occasionally also with an accessory lingual root (three to four roots total); m2 and m3 each with two small anterior roots and one large posterior root (three roots total).

Tuberculum of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; second thoracic vertebra with greatly elongated neural spine; entepicondylar foramen of humerus absent. Thoracolumbar vertebrae 19; sacrals 4; caudals 28–30, with or without hemal arches⁴; ribs 12.

Stomach (in two dissected specimens of *H. intectus*) unilocular and hemiglandular, without any extension of glandular epithelium into corpus; bordering fold crosses lesser curvature slightly to right of incisura angularis (between that flexure and the pylorus); bordering fold crosses greater curvature op-

⁴ At least one complete hemal arch (for illustrations and discussion of this character, see Steppan, 1995: 48–49) appears to be present in each of several undamaged caudal series of *Handleyomys fuscatus* that we examined, where it occurs between the second and third (ICN 12793, 12795) or between the third and fourth vertebrae (ICN 12725). However, only hemal processes (no arch) were observed in our single undamaged caudal series of *H. intectus* (ICN 12164).



Fig. 6. Maxillary tooththrows ($\times 20$) of *Handleyomys*, *Aepeomys*, and *Oryzomys*. From left to right: *Handleyomys fuscatus* (USNM 507269), *H. intactus* (ICN 16074), *Aepeomys lugens* (MBUCV I-2793), and *Oryzomys palustris* (AMNH 234936).

posite incisura angularis. Gall bladder absent (in two dissected specimens of *H. intactus*). Phallic and other male reproductive characters undetermined.

KARYOTYPE: Gardner and Patton (1976: table 2) reported a diploid number ($2n$) of 54 chromosomes and a fundamental number (FN) of 62 from three karyotyped specimens of *Handleyomys fuscatus* (USNM 507267–507269); both the X and Y chromosomes are submetacentrics (op. cit.).

COMPARISONS WITH *AEPEOMYS*: As recognized prior to this report (e.g., by Musser and Carleton, 1993; Ochoa et al., 2001), the genus *Aepeomys* contained four other nominal taxa in addition to *fuscatus*: *lugens* Thomas (1896), *vulcani* Thomas (1898), *ottleyi* Anthony (1932), and *reigi* Ochoa et al. (2001). Of these, *ottleyi* has long been considered a subjective junior synonym of *A. lugens* (see

Osgood, 1933), an assessment with which we completely agree. *Aepeomys reigi*, however, is a valid species distinguished from *A. lugens* by subtle but consistent morphological characters and by its highly distinctive karyotype (Ochoa et al., 2001). The fourth nominal taxon, *vulcani*, is based on a partially crushed holotype (BMNH 98.5.1.10) that exhibits none of the distinctive attributes shared by *A. lugens* and *A. reigi*; as independently determined by C.O. Handley, Jr. (personal commun.) and VP (in prep.), *vulcani* is referable to the genus *Thomasomys* (sensu stricto), wherein its possible synonymy with other nominal taxa remains to be determined.

Thus restricted (excluding *fuscatus* and *vulcani*), *Aepeomys* is a morphologically diagnosable taxon that can be unambiguously distinguished from *Handleyomys* despite a superficial resemblance in external features.

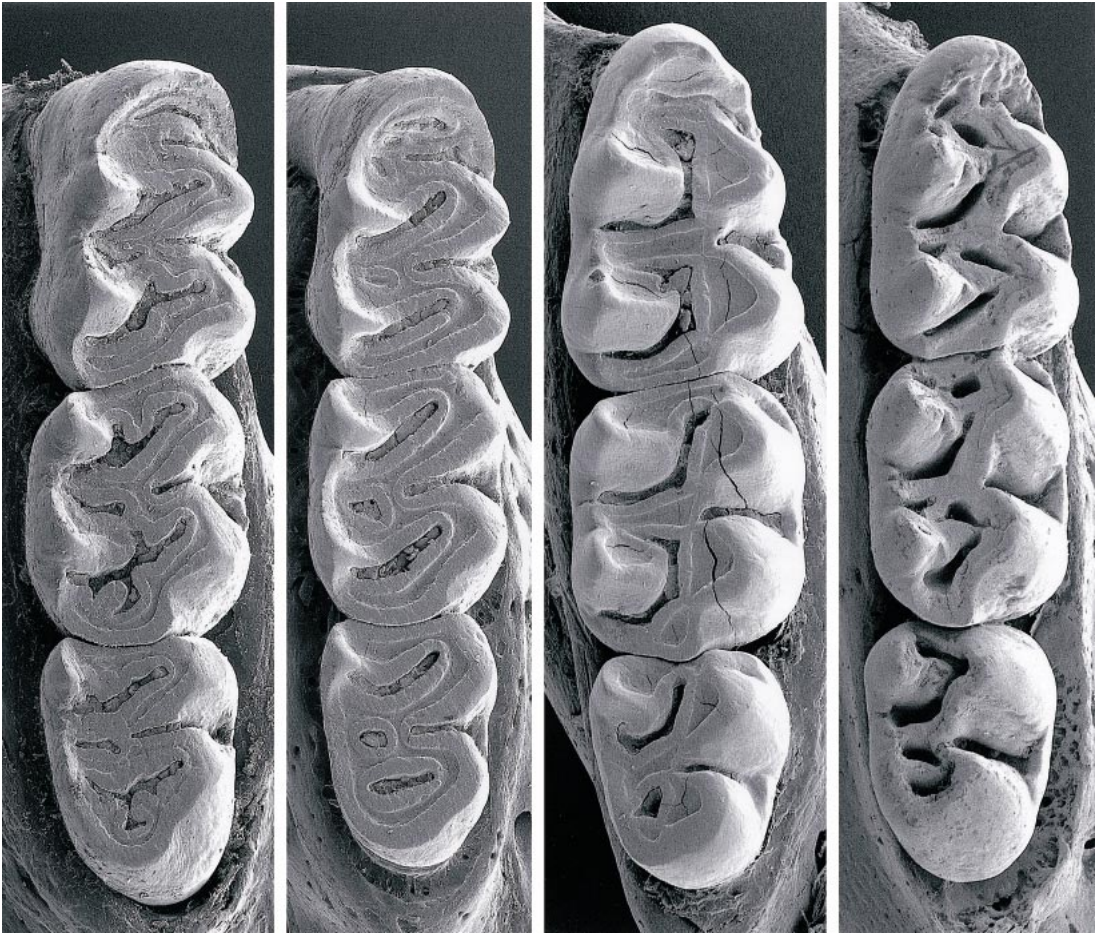


Fig. 7. Mandibular toothrows ($\times 20$) of *Handleyomys*, *Aepeomys*, and *Oryzomys*. From left to right: *Handleyomys fuscatus* (USNM 507269), *H. intactus* (ICN 16074), *Aepeomys lugens* (MBUCV I-2793), and *Oryzomys palustris* (AMNH 234936).

(Both genera include drab-colored, soft-furred mice with naked tails about as long as heads-and-bodies; narrow hindfeet with six plantar pads, short outer digits, and long ungual tufts; and six mammae.) Because field identifications of these allopatric⁵ taxa are

⁵ To date, *Aepeomys lugens* and *A. reigi* are known only from the Venezuelan Andes, where the former has been collected at elevations ranging from 1990 to 3200 m in the states of Mérida and Táchira, and the latter at 1600–3100 m in the states of Lara and Trujillo (Thomas, 1896; Anthony, 1932; Handley, 1976; Ochoa et al., 2001). Reports of *A. lugens* from Colombia (Cuervo-Díaz et al., 1986; Alberico et al., 2000) appear to have been based on misidentified material; we have not examined any Colombian material referable to this species in the AMNH, BMNH, FMNH, ICN, IAvH, MLS, USNM, or other collections.

not problematic, taxonomic comparisons are more usefully focused on their many salient points of difference in skeletal and visceral comparisons.

In dorsal and lateral cranial views (figs. 4, 5, 8) the rostrum of *Aepeomys* appears long and tapering, with a prominent bony tube formed by the nasals and premaxillae that projects anterodorsally well beyond the incisors; the rostrum of *Handleyomys* appears short and blunt by comparison, and lacks any trace of a nasal-premaxillary tube. Flanking the base of the rostrum on each side of the skull in *Handleyomys* is a shallow but well-defined zygomatic notch formed by the free anterodorsal margin of a broad, more-or-less

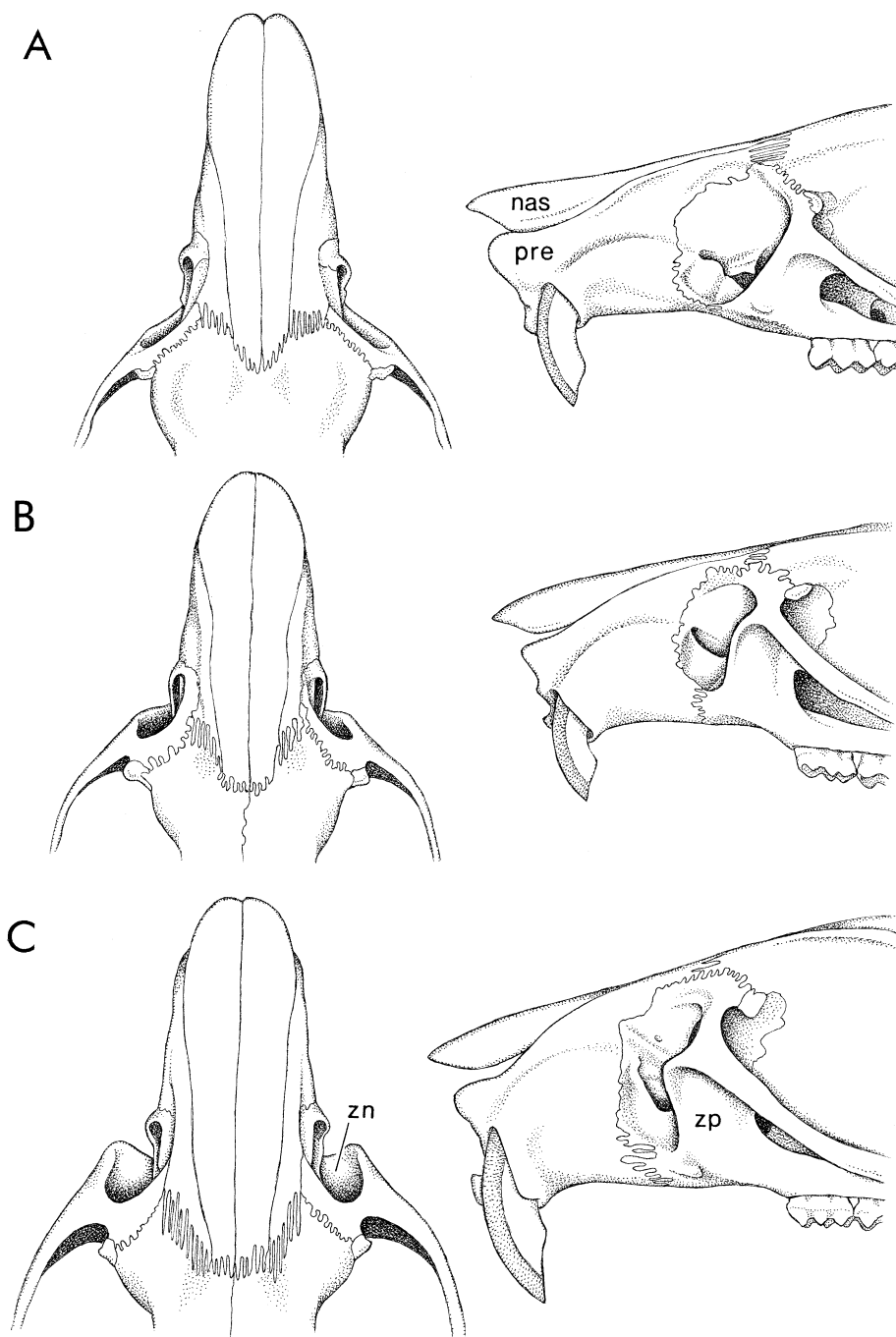


Fig. 8. Dorsal and lateral views of rostrum. **A**, *Aepeomys lugens* (AMNH 143670); **B**, *Handleyomys fuscatus* (ICN 12703); **C**, *Oryzomys palustris* (AMNH 242524). Abbreviations: **nas**, nasal; **pre**, pre-maxillary; **zn**, zygomatic notch; **zp**, zygomatic plate.

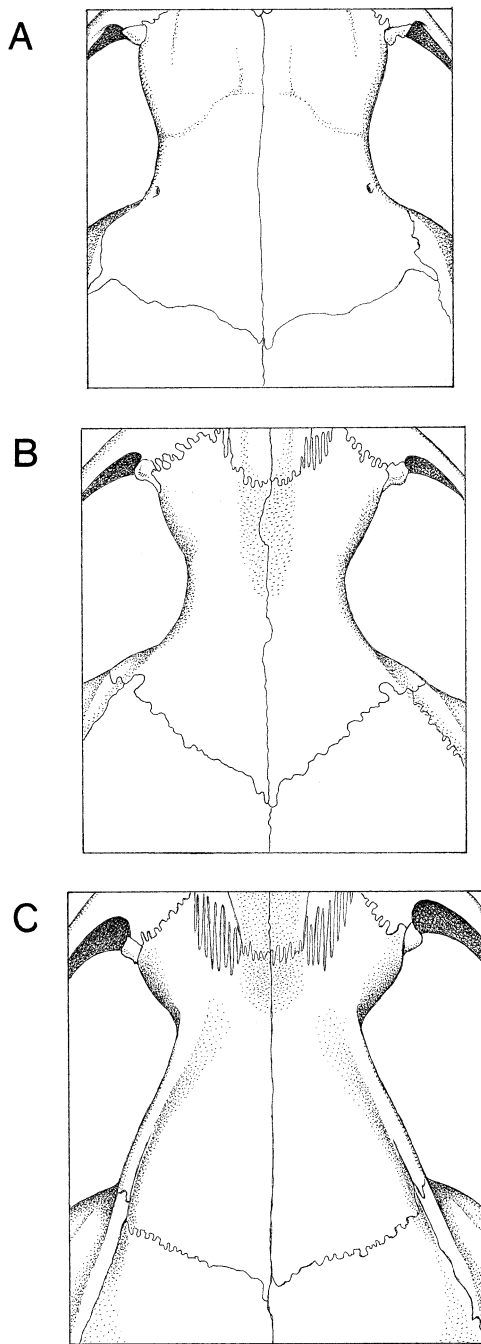


Fig. 9. Dorsal views of interorbital region. **A**, *Aepeomys lugens* (AMNH 143670); **B**, *Handleyomys fuscatus* (ICN 12703); **C**, *Oryzomys palustris* (AMNH 242524).

vertically oriented zygomatic plate. By contrast, the zygomatic notches are indistinct in *Aepeomys* because the zygomatic plate is slender and slopes posterodorsally without a free anterodorsal projection. The interorbital region is hourglass-shaped (concave-sided in dorsal view) with rounded supraorbital margins in both taxa (fig. 9A, B), but this part of the skull is relatively narrower in *Handleyomys*, a consequence of its less inflated frontal sinuses and olfactory bulb. The braincase is likewise more compact and globular in *Handleyomys* by comparison with the more inflated and ovoid calvarium of *Aepeomys*.

In ventral cranial view, the two genera are most conspicuously distinguished by palatal morphology. Whereas the palate of *Aepeomys* is relatively short (not extending posteriorly much behind the molar rows) and lacks well-developed posterolateral pits (fig. 10A), the palate of *Handleyomys* is long (extending posteriorly well behind the molar rows) and is perforated posterolaterally by one or more large pits between M3 and the mesopterygoid fossa (fig. 10B). In addition, the wide mesopterygoid fossa of *Aepeomys* is flanked by long, narrow parapterygoid fossae, but the mesopterygoid fossa of *Handleyomys* is relatively narrower and flanked by shorter, broader parapterygoid fossae; in both genera, the mesopterygoid roof is entirely bony or is perforated only by small foramina.

In *Aepeomys*, the bulla is firmly anchored to the rest of the skull anterodorsally by broad overlap between the tegmen tympani and a posterior suspensory process of the squamosal, and the postglenoid foramen (through which the eponymous vein exits the cranial lumen) is smaller than the subsquamosal fenestra (fig. 11A). By contrast, the bulla of *Handleyomys* is not firmly anchored to the skull anterodorsally because the squamosal lacks a posterior suspensory process; in consequence, the postglenoid foramen is much wider than the subsquamosal fenestra (fig. 11B).

The upper molar dentitions of both genera are highly distinctive (fig. 6). The first maxillary molar of *Aepeomys* is relatively longer and narrower than the shorter, broader M1 of *Handleyomys*, and the unworn labial cusps (paracone and metacone) of M1–M2 in *Aepeomys* are much taller and sharper than their

homologs in *Handleyomys*. With increasing toothwear, the principal molar cusps of *Aepeomys* persist as distinct tubercles, whereas the molar cusps of *Handleyomys* are quickly worn down to form a common planar surface with other occlusal features. Differences in the length and orientation of the principal labial and lingual flexi are also striking. In *Aepeomys*, the internal segments of the major labial folds (paraflexus and metaflexus) are oriented anteroposteriorly down the midline of M1–M2, and the lingual flexi (protoflexus and hypoflexus) are shallow; longitudinal (rather than transverse) enamelled crests are therefore prominent in these teeth. By contrast, the principal labial flexi of *Handleyomys* slant transversely across the midline of the tooth to interpenetrate with much longer lingual flexi, resulting in the morphology that Voss (1993: 20) termed “incipient lophodonty”. The unworn anterocone of M1 is deeply divided by an anteromedian flexus in *Aepeomys*, whereas the M1 anterocone is undivided in *Handleyomys*. Corresponding differences are apparent in the lower molars as well (fig. 7).

Whereas 13 ribs have been reported for *Aepeomys lugens* (see Steppan, 1995: table 5), all examined postcranial skeletons of *Handleyomys fuscatus* (ICN 12786) and *H. intectus* (ICN 12160, 12164) have 12 ribs.

Visceral differences that we observed between dissected examples of *Aepeomys lugens* (MBUCV I-2793, I-2794) and *Handleyomys intectus* (ICN 16092, 16093) include gastric morphology and occurrence of a gall bladder. The stomachs of both genera are unilocular (single-chambered), but gastric glandular epithelium in *Aepeomys* is restricted to a small, pouch-like structure on the greater curvature (closely resembling the condition illustrated by Carleton [1973: fig. 5C] for *Oxymycterus rutilans*). By contrast, the entire right half (antrum) of the stomach is lined with glandular epithelium in *Handleyomys* (closely resembling the hemiglandular condition illustrated by Carleton [1973: fig. 2D] for *Zygodontomys brevicauda*). A large and distinct gall bladder is present in a cleft between the left and right halves of the cystic lobe of the liver in *Aepeomys* (as previously reported by Voss, 1991: table 4), but both

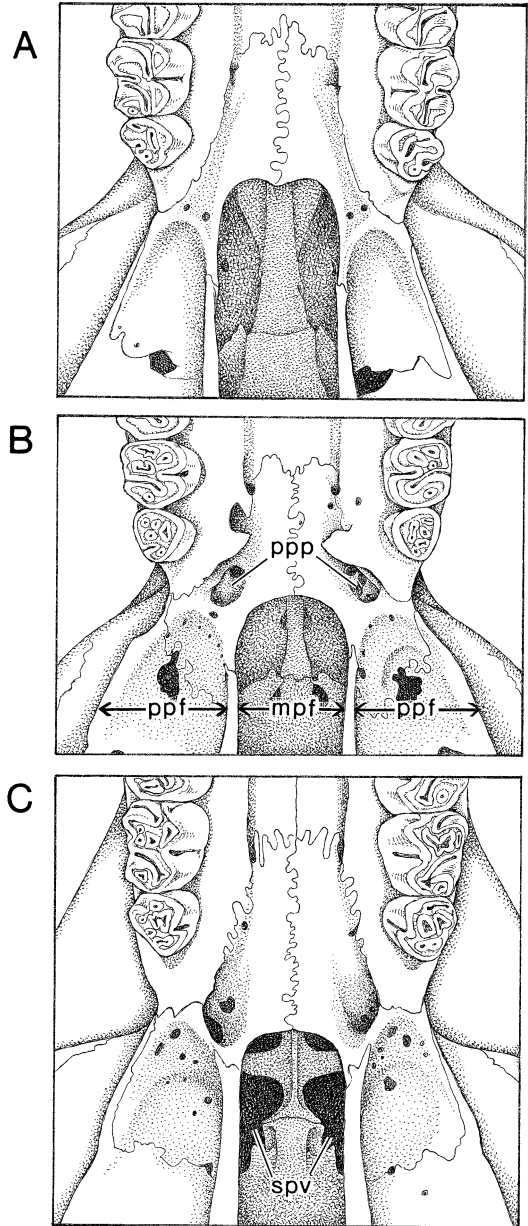


Fig. 10. Ventral views of posterior palate and mesopterygoid fossa. **A**, *Aepeomys lugens* (USNM 579520); **B**, *Handleyomys intectus* (ICN 16092); **C**, *Oryzomys palustris* (AMNH 242524). Abbreviations: **mpf**, mesopterygoid fossa; **ppf**, parapterygoid fossa; **ppp**, posterolateral palatal pits; **spv**, sphenopalatine vacuities.

dissected specimens of *Handleyomys* lack a gall bladder.

COMPARISONS WITH *ORYZOMYS*: Even excluding *intectus*, the genus *Oryzomys* remains a morphologically heterogeneous collection of species that defies meaningful diagnosis. Because several systematic studies have recently suggested that *Oryzomys*—even in its strict modern sense (Musser and Carleton, 1993)—is not monophyletic (see Myers et al., 1995; Steppan, 1995; Weksler, 1996; Bonvincino and Moreira, 2001), we base our comparisons on a small group of taxa that appear to be closely related to the type species, *O. palustris* (Harlan). This core concept of *Oryzomys* essentially corresponds to Goldman's (1918) *palustris* group and additionally includes *O. couesi* (Alston), *O. dimidiatus* (Thomas), *O. gorgasi* Hershkovitz, and other possibly valid species currently regarded as synonyms of *O. couesi* (see Sánchez et al., 2001). In the following paragraphs we use *Oryzomys* in this narrowly defined sense, acknowledging that additional genera must eventually be named to contain at least some of the many other species currently referred to this long-abused taxon. Carleton and Musser (1989) provided detailed illustrations and descriptions of many morphological traits of *O. palustris* that should be consulted for additional details of characters mentioned below.

Species of *Oryzomys* are much more boldly marked externally—with abruptly countershaded heads and bodies and sharply bicolored tails—than species of *Handleyomys*, which lack distinct countershading and have unicolored-dark tails. Whereas the plantar surface of the hindfoot is almost entirely covered with squamae and the hypothenar (lateral tarsal) pad is indistinct or absent in *Oryzomys* (see Carleton and Musser, 1989: fig. 9A), squamae are only present on the outer distal margins of the sole and the hypothenar pad is distinct in *Handleyomys* (fig. 3). Although well-developed fringes of silvery hairs are present along the plantar margins of the hindfoot, the claws are naked in *Oryzomys*; by contrast, no conspicuous hairy fringes occur along the plantar margins, but the claws on digits II–V are concealed by long tufts of ungual hairs in *Handleyomys*. Additionally, *Oryzomys* has eight mammae in four

pairs (inguinal, abdominal, postaxial, and pectoral), but *Handleyomys* has only six teats in three pairs (the pectoral pair is absent; see Voss and Carleton [1993: fig. 8] for a map of muroid mammary loci).

Oryzomys is cranially distinctive by virtue of its deep zygomatic notches (the zygomatic notches are distinct but much shallower in *Handleyomys*; fig. 8), convergent interorbital region with beaded supraorbital margins (the interorbit is hourglass-shaped with rounded margins in *Handleyomys*; fig. 9), widely fenestrated mesopterygoid roof (the mesopterygoid roof is entirely bony or only narrowly perforated by sphenopalatine openings in *Handleyomys*; fig. 10), and highly derived (pattern 3) carotid circulation (versus pattern 1 in *Handleyomys*; see Voss [1988: fig. 18] for illustrated examples and explanations of these morphologies). The lower incisor root is contained in a prominent bony capsule on the lateral surface of the mandible below the base of the coronoid process in *Oryzomys*, but a distinct capsular process is absent in *Handleyomys*. Whereas the molar dentition of *Oryzomys* is persistently tubercular and nonlophodont, the principal cusps of *Handleyomys* molars are quickly worn down to a flat (planar) occlusal surface dominated by interpenetrating labial and lingual flexi (conforming to the incipiently lophodont morphotype defined by Voss [1993: 20]).

Despite the many points of external and craniodental difference noted above, *Oryzomys* and *Handleyomys* resemble one another in all postcranial-skeletal and visceral characters scored for this report. In particular, both taxa have 12 ribs and unilocular-hemiglandular stomachs; the gall bladder is likewise absent in each genus.

PHYLOGENETIC RELATIONSHIPS AND OTHER COMPARISONS: Pentalophodont sigmodontines—those with well-developed mesoloph(id)s—have traditionally been referred to one or the other of two suprageneric groups: one cluster including *Thomasomys* and its putative allies (“thomasomyines”), the other *Oryzomys* and its supposed relatives (oryzomyines; see Voss [1993: 21–25] for a historical review of this dichotomy). Although any discussion of the relationships of *Handleyomys* in this report will soon be superseded by taxon-dense phylogenetic analyses of

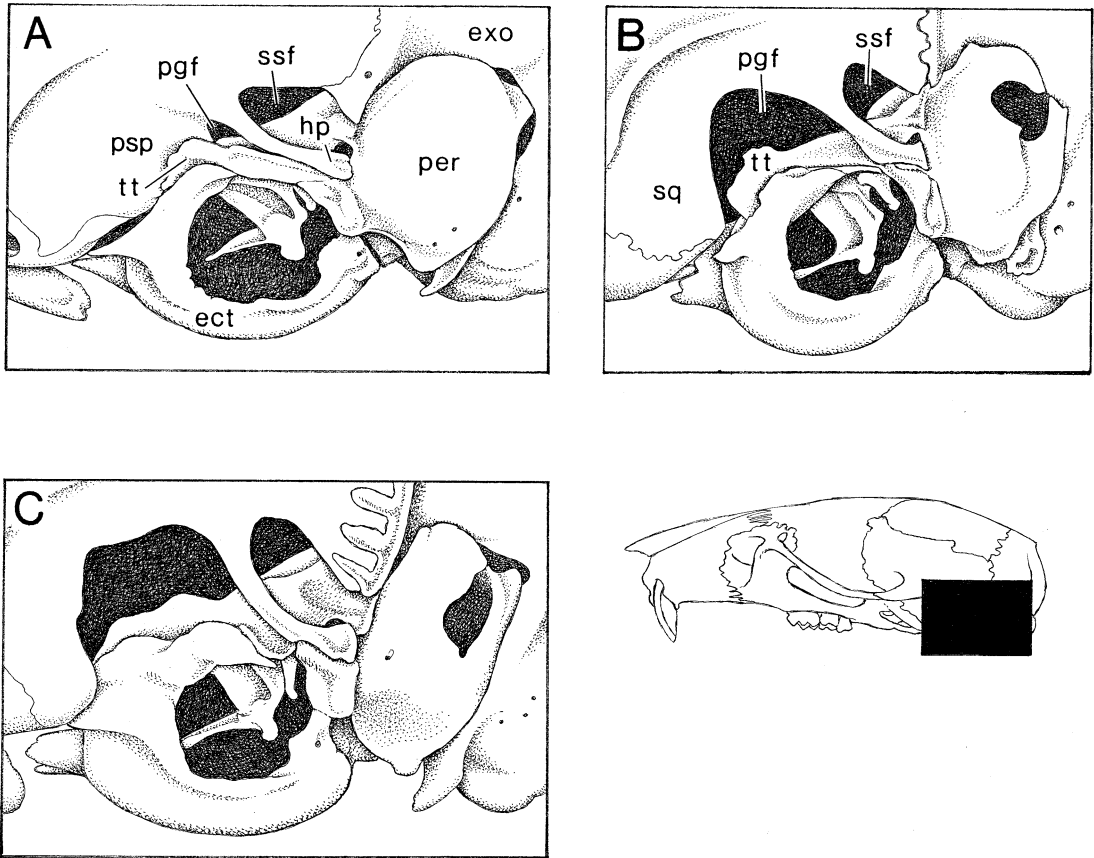


Fig. 11. Left lateral views of auditory region. **A**, *Aepeomys lugens* (MBUCV 2793); **B**, *Handleyomys intectus* (ICN 16079); **C**, *Oryzomys palustris* (AMNH 242519). Abbreviations: **ect**, ectotypanic; **exo**, exoccipital; **hp**, hamular process of squamosal; **per**, petriotic capsule of petrosal; **pgf**, postglenoid foramen; **psp**, posterior suspensory process of squamosal; **sq**, squamosal; **ssf**, subsquamosal fenestra; **tt**, tegmen tympani (of petrosal).

“thomasomyines” (by VP) and oryzomyines (by M. Weksler) that are currently nearing completion, some preliminary remarks about the data at hand are appropriate.

Among those morphological characters with well-defined states for which hypotheses of polarity have been proposed in the literature (table 1), it is noteworthy that none supports a close relationship between *Aepeomys* (a “thomasomyine”) and *Handleyomys*. Instead, all of the tabulated character states shared by these taxa appear to be plesiomorphic on the basis of current assessments of evolutionary transformations in sigmodontine morphology. Likewise, we found no compelling evidence of recent common an-

cestry between *Aepeomys* and *Handleyomys* among characters that we do not tabulate, most of which have less well-defined states and/or more ambiguous polarity.

In contrast, *Handleyomys* shares an impressive number of shared-derived resemblances with *Oryzomys*, including (1) a long palate with large posterolateral pits; (2) absence of overlap between the tegmen tympani and a posterior suspensory process of squamosal; (3) absence of an anteromedian flexus on M1; (4) 12 ribs; and (5) absence of a gall bladder. Because traits 1, 2, 4, and 5 are currently thought to be oryzomyine synapomorphies (Voss and Carleton, 1993; Stepan, 1995), we hypothesize that *Handleyo-*

TABLE 1
Morphological Comparisons Among *Aepeomys*, *Handleyomys*, and *Oryzomys*

Characters ^a	<i>Aepeomys</i> ^b	<i>Handleyomys</i>	<i>Oryzomys</i> ^c
Ungual tufts:	present	present	<i>absent</i>
Plantar pads:	six	six	<i>five</i>
Mammae:	six	six	<i>eight</i>
Rostral tube:	<i>present</i>	absent	absent
Zygomatic notch:	indistinct	shallow	<i>deep</i>
Zygomatic plate:	<i>narrow & sloping</i>	broad & vertical	broad & vertical
Interorbital region:	"hourglass", with rounded margins	"hourglass", with rounded margins	<i>convergent with beaded margins</i>
Palate:	short, without large posterolateral pits	<i>long, with large posterolateral pits</i>	<i>long, with large posterolateral pits</i>
Mesopterygoid fossa:	not fenestrated	not fenestrated	<i>fenestrated</i>
Carotid circulation:	pattern 1	pattern 1	<i>pattern 3</i>
Tegmen tympani:	overlaps squamosal	<i>no squamosal overlap</i>	<i>no squamosal overlap</i>
Capsular process:	absent	absent	<i>present</i>
Molar design:	not lophodont	<i>incipiently lophodont</i>	not lophodont
Anteromedian flexus:	present	<i>absent</i>	<i>absent</i>
Number of ribs:	thirteen	<i>twelve</i>	<i>twelve</i>
Stomach:	<i>discoglandular</i>	hemiglandular	hemiglandular
Gall bladder:	present	<i>absent</i>	<i>absent</i>

^a Italicized character states are hypothesized to be derived within the Neotropical murid subfamily Sigmodontinae as reviewed and discussed by Voss (1993) and Steppan (1995); see text for additional explanation and discussion.

^b Tabulated character states are those of *Aepeomys lugens*, the type species.

^c Tabulated character states are those of *Oryzomys palustris*, the type species.

mys is a member of that clade, within which other taxonomic comparisons are appropriate. Three oryzomyine genera deserve particular attention.

In his original description of *Oryzomys intectus*, Thomas (1921) compared it with *Melanomys*, remarking general similarities in cranial shape and molar morphology. However, species of *Melanomys* differ from *Handleyomys* by their coarser, glossier, more richly colored (usually chestnut- or reddish-brown) pelage; relatively shorter tail (LT < HBL); shorter hindfeet with blackish soles and large, almost-naked claws; mammary complement of eight teats; relatively shorter rostrum; relatively broader, convergent-beaded interorbit; relatively much narrower parapterygoid fossae; highly derived (pattern 3) carotid circulation; lack of subsquamosal fenestrae; and narrower, nonlophodont molars (see Goldman [1918, 1920] for descriptions

and illustrations). In fact, we have not found a single trait in which *Melanomys* and *Handleyomys* resemble one another that is not also shared with many other small oryzomyines. Prima facie, they do not appear to be closely related.

Ellerman (1941: 341) astutely noted the "highly aberrant dentition" of *Oryzomys intectus* with respect to other congeners, and remarked that "... this species should, I think, be transferred to the genus *Nectomys*." Although the incipiently lophodont molars of *Handleyomys* (figs. 6, 7) and *Nectomys* (see Hershkovitz, 1944: fig. 4; Gómez-Laverde et al., 1999: fig. 4) are a noteworthy point of shared-derived resemblance, these genera are dissimilar in most other respects. Species of *Nectomys* are much larger rats (adult HBL > 160 mm) that differ from *Handleyomys* in many external and craniodental traits, including their coarser, glossier, water-repellent fur;

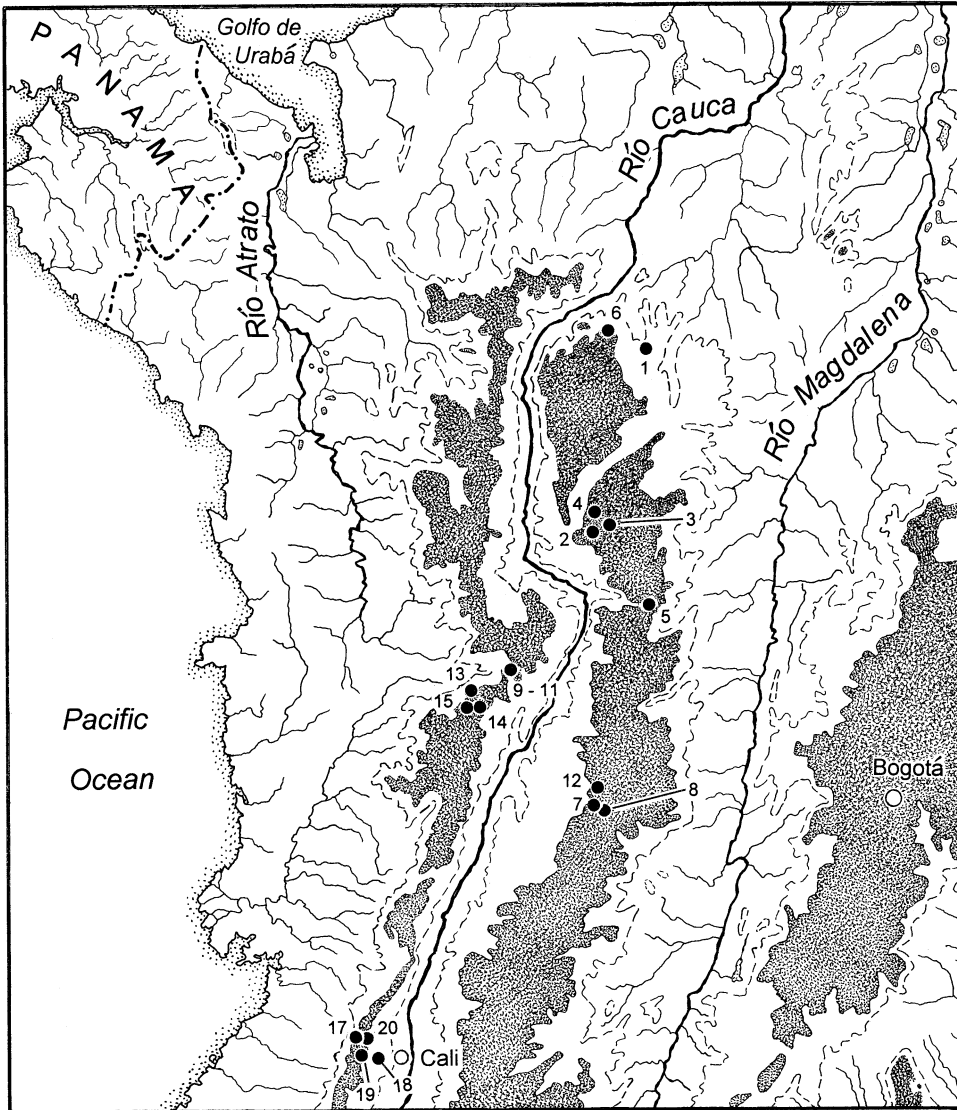


Fig. 12. Geographic distribution of *Handleyomys* in the western Andes (Cordillera Occidental) and central Andes (Cordillera Central) of Colombia based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix). The 1000 m contour is indicated with a broken line; elevations above 2000 m are densely stippled. The western Andes are west of the Río Cauca, and the central Andes are between the Río Cauca and the Río Magdalena; the mountains east of the Río Magdalena are the eastern Andes (Cordillera Oriental). The frame of reference is approximately 3°10'–9°00' N and 73°30'–78°20' W. Locality 16 is adjacent to localities 17–20 but lacks definite geographic coordinates and is not plotted.

relatively longer tail ($LT > HBL$); very large hind feet with prominent plantar squamae, well-developed interdigital webbing, and naked claws (Hershkovitz, 1944: fig. 2c, d);

mammary complement of eight teats; relatively shorter rostrum; much deeper zygomatic notches and correspondingly broader zygomatic plates; convergent-beaded inter-

orbit; highly derived (pattern 3) carotid circulation; and lack of subsquamosal fenestrae. That Ellerman did not, in fact, transfer *intectus* from *Oryzomys* to *Nectomys* probably resulted from the lack of supporting evidence from other (nonmolar) characters.

Although Voss and Carleton (1993) stated that all oryzomyines possess eight mammae in four pairs (inguinal, abdominal, postaxial, and pectoral), subsequent research has shown that the oryzomyine genus *Scolomys* is characterized by having only six teats because the pectoral mammary pair is absent (Patton and da Silva, 1995). *Handleyomys* likewise has only six teats (lacking pectoral mammae), but the phylogenetic interpretation of this similarity is ambiguous. Six mammae are thought to represent the plesiomorphic condition among Neotropical sigmodontines (according to the ingroup and outgroup assumptions explained by Voss, 1993: 12), so the shared possession of this primitive feature by *Scolomys* and *Handleyomys* suggests that these genera might be basal to an oryzomyine radiation of eight-mammate taxa. Alternatively, if *Scolomys* and *Handleyomys* are descended from an oryzomyine ancestor with eight teats, their shared loss of pectoral mammae provides evidence of a sister-group relationship. Obviously, distinguishing between these (and other) alternatives is impossible in the absence of a comprehensive analysis of oryzomyine phylogeny, but it is relevant that no other special similarities suggest a close relationship between *Scolomys* and *Handleyomys*.

Indeed, no oryzomyine genus appears to exhibit any compelling pattern of synapomorphies with *Handleyomys* apart from those that support tribal monophyly. Likewise, none of the morphologically diverse species currently referred to *Oryzomys* (sensu Musser and Carleton, 1993) seems to show any special morphological similarity with *H. fuscatus* or *H. intectus*. Given the Linnaean convention of binomial nomenclature and the absence of evidence for close relationship to other oryzomyines, we treat *Handleyomys* as a genus, but we acknowledge that assigning ranks to supraspecific clades is a biologically arbitrary exercise. Determining the hierarchical position of this taxon with respect to other sigmodontine lineages is the key issue,

and one that remains to be determined by future phylogenetic studies.

GEOGRAPHIC VARIATION AND SPECIES LIMITS

All of the material of *Handleyomys* that we examined comes from elevations above 1500 m in the western Andes (Cordillera Occidental) and central Andes (Cordillera Central) of Colombia. Because the cool, humid habitats that prevail above 1500 m in these mountain ranges are separated by the hot, semi-arid lowlands of the upper Río Cauca (fig. 12), we tested the hypothesis that populations of *Handleyomys* in the western Andes (including the type locality of *fuscatus*) are morphologically distinct from allopatric populations in the central Andes (including the type locality of *intectus*).

Close visual inspection of skins and skulls from both regions revealed three qualitative characters that exhibit significant geographic variation in trait frequencies. (1) The short hairs that cover the dorsal surface of the hind feet are *dark-banded* (with dense concentrations of melanin that are distinctly visible under low magnification) in all examined specimens from the western Andes, but most specimens from the central Andes have hind feet that are covered dorsally with *pale* (pure-white or indistinctly pigmented) hairs. (2) The nasal bones are *long* (extending posteriorly well beyond the premaxillary-maxillary suture; fig. 13B) in most examined specimens from the central Andes, whereas most specimens from the western Andes have *short* nasals (truncated posteriorly at or near the premaxillary-maxillary suture; fig. 13A). (3) The incisive foramina are *anteriorly constricted* (with lateral margins that are abruptly narrowed at or near the premaxillary-maxillary suture; fig. 14A) in most specimens from the western Andes, but these diastemal openings are *smoothly tapering* (with evenly rounded lateral margins like parentheses; fig. 14B) in most specimens from the central Andes. Although none of these characters exhibits fixed differences between western and central Andean samples (table 2), it is noteworthy that no examined specimen is geographically atypical in all three scored traits. Thus, no specimen from the western Andes has pale hind feet, long nasal

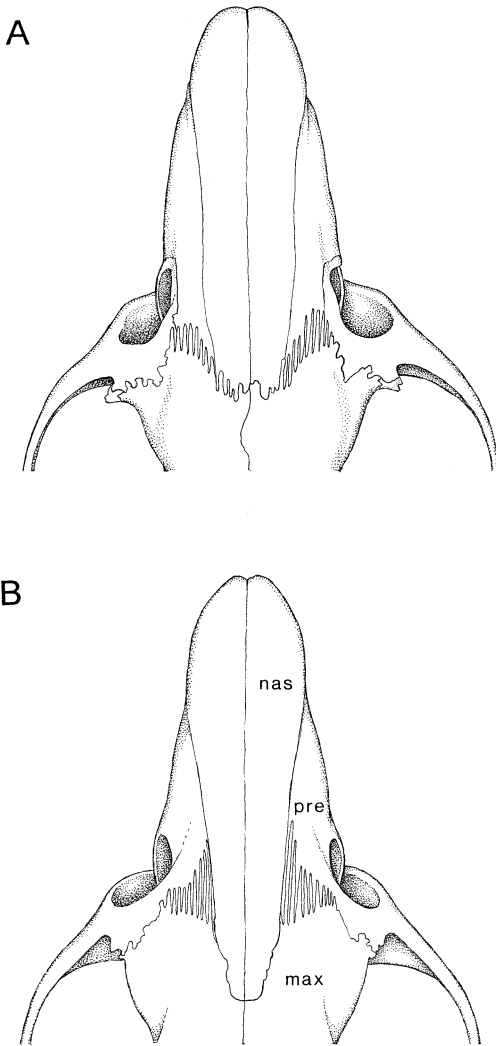


Fig. 13. Typical morphology of the nasal bones in *Handleyomys fuscatus* (A, ICN 12701) and *H. intectus* (B, ICN 16074). In *H. fuscatus*, the nasals (**nas**) are usually short because they are truncated abruptly at or near the sutures between the premaxillary (**pre**) and maxillary (**max**) bones. In *H. intectus*, the nasals are usually longer because they extend posteriorly beyond the premaxillary-maxillary sutures.

bones, and smoothly tapering incisive foramina; nor does any specimen from the central Andes have dark hind feet, short nasal bones, and anteriorly constricted incisive foramina. Therefore, these aggregate data suggest that the two cordilleras are inhabited by morpho-

logically distinctive populations of *Handleyomys*.

We also calculated summary statistics for external and craniodental measurements of adult *Handleyomys* to assess univariate patterns of morphometric divergence between populations from the western and central Andes (table 3). External measurement means appear to be similar from the two cordilleras, but we did not apply statistical tests because specimens were measured in the field by many different persons (including inexperienced undergraduates) using unknown protocols. We used one-way Analyses of Variance, however, to test for sample differences in craniodental measurements, all of which were taken by us using identical methods. No significant differences were found between cordilleran samples in Condylar Incisive Length, Length of Diastema, Breadth of Incisive Foramina, Breadth of Palatal Bridge, and Zygomatic Breadth. Other craniodental measurements showed statistically significant differences, but some of these are not empirically compelling (e.g., BM1 and LIB, with mean differences < 0.01 mm). The most visually obvious differences indicated by these tests are in Length of Nasals (already scored as a qualitative trait; table 2, fig. 12), and Interparietal Breadth. Although the latter measurement exhibits slight overlap between western and central Andean specimens (8.2–10.2 mm versus 6.2–8.8 mm, respectively), the mean morphological difference is obvious when skulls are viewed side-by-side (fig. 15). Contrasts between western and central Andean skulls in Molar Length, Length of the Incisive Foramina, and Breadth of the Zygomatic Plate are visually subtle in some pairwise comparisons of local population samples but visually conspicuous in others (see below).

To summarize geographic patterns of multivariate morphometric variation, we calculated Mahalanobis distances (D) among five geographic samples, two from the western Andes and three from the central Andes (table 4). In general, morphometric distances between geographic samples from the same cordillera are smaller than distances between samples from different cordilleras, a pattern that can be heuristically summarized by cluster analysis (fig. 16). Because some sample

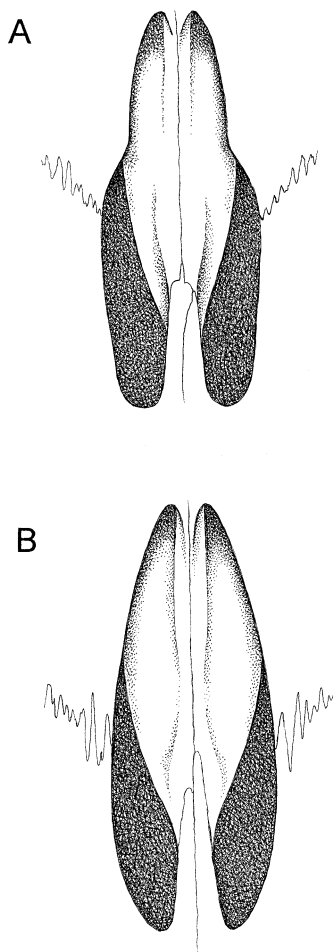


Fig. 14. Typical morphology of the incisive foramina in *Handleyomys fuscatus* (A, ICN 12701) and *H. inectus* (B, ICN 16074). The foramina are usually abruptly constricted anteriorly (at or near the premaxillary-maxillary sutures) in *H. fuscatus*, but the foraminal margins of *H. inectus* are usually smoothly tapering (resembling parentheses), without any abrupt change of curvature. An intermediate morphology is exhibited by occasional specimens of both species.

sizes are small, clustering sequences determined by small differences in computed distances (e.g., within the central Andean cluster) are probably not biologically significant, and some large values (e.g., between Valle del Cauca and Western Risaralda) might be artifactually inflated. Nevertheless, the substantial estimated mean distance between

western and Central Andean samples (ca. 6.5 within-sample multivariate standard deviations) reinforces the conclusion previously based on qualitative character data that these mountain ranges are occupied by morphologically differentiated populations of *Handleyomys*.

A valid criticism of cluster-analytic summaries of geographic variation is that hierarchical patterns are forced on data that may not, in fact, be hierarchically structured (de Queiroz and Good, 1997). In particular, discontinuous variation (as resulting from speciation) cannot be distinguished by cluster analysis from intraspecific clinal variation without taking the geographic distribution of the analyzed samples into consideration (op. cit.). Intraspecific clinal variation is not, however, a plausible explanation for our results, because geographic and morphometric distances are not correlated in *Handleyomys*. The Quindío/eastern Risaralda sample, for example, clusters with geographically distant samples from Antioquia rather than with the geographically adjacent sample from western Risaralda (just across the Cauca valley). Nevertheless, it is possible that such geographically proximate but morphometrically divergent populations of *Handleyomys* might show some degree of intergradation.

To further assess the distinctness of adjacent western Andean versus central Andean populations, we used principal components analysis to summarize patterns of multivariate craniometric variation in our samples from El Campamento (in western Risaralda; locality 14) and La Suiza (in eastern Risaralda; locality 12). The first two principal components account for about 75% of the total variance (table 5). Projected specimen scores (fig. 17) indicate complete sample separation on the first component, the coefficients of which suggest that La Suiza specimens differ from El Campamento specimens by their longer incisive foramina, narrower zygomatic plates, longer nasals, and narrower interparietals (essentially the same pattern of morphometric divergence previously identified by our univariate comparisons of central versus western Andean series). The second principal component appears to represent a general size factor, with coefficients that resemble the usual muroid pattern of multi-

variate craniodental growth allometry (Voss et al., 1990; Voss and Marcus, 1992).⁶

We interpret these results as indicating the presence of two species of *Handleyomys*, one in the western Andes and the other in the central Andes, despite the apparent absence of any completely fixed qualitative character difference. Fortunately, names are already available for both taxa: *H. fuscatus* for the populations inhabiting the Cordillera Occidental, and *H. intectus* for populations in the Cordillera Central. We briefly summarize the distinguishing attributes of each taxon in the following accounts.

Handleyomys fuscatus (J.A. Allen, 1912)

Aepeomys fuscatus J.A. Allen, 1912: 89.

Thomasomys fuscatus: Ellerman, 1941: 369 (new name combination).

Thomasomys lugens fuscatus: Cabrera, 1961: 431 (new name combination).

TYPE MATERIAL AND TYPE LOCALITY: Allen's (1912) original description was based on the holotype (AMNH 32230, preserved as a skin and skull) and 11 paratypes, all of which were collected between 7000 and 8000 ft near San Antonio, Valle del Cauca, Colombia, by W.B. Richardson from 5 January to 31 March 1911.

GEOGRAPHIC DISTRIBUTION: All referred specimens of *Handleyomys fuscatus* are from the western Andes (Cordillera Occidental) of Colombia between 1700 and 2580 m above sea level in the departments of Valle del Cauca and Risaralda.

EMENDED DIAGNOSIS: A species of *Handleyomys* distinguished by hindfeet that are covered dorsally with dark-banded (never pure-white) hairs; nasals that are usually truncated

TABLE 2
Comparisons of Qualitative Character-State Frequencies Between *Handleyomys* Samples from the Central and Western Andes^a

	Central	Western
<i>Hindfoot coloration:</i>		
Dark	10	65
Pale	38	0
$p < 0.01$		
<i>Nasal bones:</i>		
Long	42	18
Short	1	48
$p < 0.01$		
<i>Incisive foramina:</i>		
Anteriorly constricted	0	44
Intermediate	7	15
Smoothly tapering	35	6
$p < 0.01$		

^a Specimens scored for these comparisons are nonsenescent adults (corresponding to age classes 2–4 of Voss, 1991). See text for character definitions and scoring conventions. All relevant tests of association (chi-square, likelihood ratio chi-square, Fisher's exact method) give essentially equivalent results with these data.

posteriorly at or near the premaxillary-maxillary suture; incisive foramina with lateral margins that are usually constricted abruptly anteriorly; and wide-shallow interparietals.

VARIATION: All of the material at hand of *Handleyomys fuscatus* comes from two clusters of adjacent localities, one of which is near Cali in the department of Valle del Cauca and the other in western Risaralda department. Although univariate mean differences between samples from these regions are not impressive (table 6), it is noteworthy that the pattern of divergence is not attributable to a simple size factor. Whereas specimens from Valle del Cauca average larger than specimens from western Risaralda in several dimensions (e.g., CIL, LD, LIB, ZB, IPB), the same specimens have absolutely and relatively smaller incisive foramina (LIF, BIF), more slender zygomatic plates (BZP), and shorter nasals (NL). Because only a few measurable adults are available from Valle del Cauca, it is possible that some of these differences are artifactual, but the estimated multivariate distance between Valle del Cauca and western Risaralda (>5 within-sample

⁶ In most principal components analyses of closely related murid species, neither PC1 nor PC2 (computed from the total covariance matrix of log-transformed measurements) are biologically interpretable because taxa usually differ in both size and shape. Therefore, factors representing general size (the result of postweaning growth) and growth-invariant shape differences are typically oblique to the principal component axes and must be modeled explicitly (see Voss et al. [1990] and Voss and Marcus [1992] for relevant discussions and examples). In the present application, explicit modeling is unnecessary because *Handleyomys fuscatus* and *H. intectus* appear to differ only in growth-invariant cranial proportions, which clearly account for the largest axis of dispersion in the total covariance matrix.

TABLE 3
Summary Statistics^a for External and Craniodental Measurements (in millimeters)
and Weights (in grams) of Adult *Handleyomys* from the Western and Central Andes

	Western Andes ^b	Central Andes ^c	Difference ^d
HBL	98 ± 8 (80–130) 61	102 ± 7 (85–114) 47	—
LT	91 ± 8 (75–110) 61	95 ± 7 (75–106) 47	—
HF	24 ± 1 (22–26) 66	24 ± 1 (21–26) 50	—
Ear	14 ± 1 (10–17) 54	14 ± 2 (10–17) 43	—
CIL	23.8 ± 0.8 (21.6–25.8) 62	23.9 ± 1.1 (21.0–25.5) 44	ns
LD	7.1 ± 0.4 (6.1–8.3) 66	7.2 ± 0.4 (5.9–7.9) 50	ns
LM	4.3 ± 0.1 (4.0–4.6) 66	4.1 ± 0.1 (3.8–4.4) 51	***
BM1	1.3 ± 0.1 (1.2–1.4) 66	1.3 ± 0.0 (1.2–1.4) 51	*
LIF	4.2 ± 0.3 (3.4–4.8) 66	4.5 ± 0.2 (3.8–5.0) 50	***
BIF	2.0 ± 0.2 (1.7–2.8) 65	2.0 ± 0.1 (1.7–2.2) 50	ns
BPB	2.7 ± 0.2 (2.2–3.2) 64	2.8 ± 0.2 (2.2–3.1) 50	ns
BZP	2.4 ± 0.2 (1.9–2.8) 66	2.2 ± 0.2 (1.8–2.6) 50	***
LIB	4.9 ± 0.2 (4.5–5.3) 66	4.9 ± 0.2 (4.6–5.3) 51	*
ZB	13.8 ± 0.5 (12.6–15.3) 52	14.0 ± 0.5 (12.8–14.9) 42	ns
NL	10.4 ± 0.5 (8.9–11.5) 64	11.2 ± 0.6 (9.5–12.5) 45	***
IPB	9.2 ± 0.5 (8.2–10.2) 62	7.6 ± 0.6 (6.2–8.8) 46	***
Weight	26 ± 4 (19–34) 53	26 ± 4 (17–33) 25	—

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size.
^b Cordillera Occidental; see footnotes to table 6 for list of measured specimens.
^c Cordillera Central; see footnotes to table 7 for list of measured specimens.
^d Results of one-way ANOVAs testing for mean differences between samples from the western and central cordilleras. Abbreviations: ns, not significant; *, $p < 0.05$; ***, $p < 0.001$.

standard deviations; fig. 16) is larger than that observed between any other conspecific pair of samples analyzed in this report and suggests that substantial genetic variation might exist among *Handleyomys* populations from the Cordillera Occidental. In the current absence of other supporting evidence, it does not seem necessary or useful to recognize more than a single taxon in the western Andes, but future karyotypic and molecular datasets should be carefully assessed for geographic variation among populations here referred to *H. fuscatus*.

SPECIMENS EXAMINED: *Risaralda*, El Campamento (ICN 12799–12827), El Empalado (ICN 12700–12703, 12705–12710), La Jalea (ICN 12704), Los Planes (ICN 12783–12793, 12795–12798), Mampay (ICN 15277), Siató (ICN 12208, 12725–12727); *Valle del Cauca*, Campamento Corea (IND-M 3657, 3659), El Queremal (ICN 6903), Finca la Playa (ICN 4376, 4381, 4383, 4388, 4389), Peñas Blancas (USNM 507267–507269), San Antonio (AMNH 32227–32233, 32236–32239; FMNH 20109).

Handleyomys intectus (Thomas, 1921)

Oryzomys intectus Thomas, 1921: 356.
Oryzomys (Oryzomys) intectus: Tate, 1932a: 16 (new name combination).
?Nectomys intectus: Ellerman, 1941: 351 (suggested name combination).

TYPE MATERIAL AND TYPE LOCALITY: Thomas’s (1921) original description was based on the holotype (BMNH 21.7.1.17, preserved as a skin and skull) and two paratypes, all of which were collected at Santa Elena, near Medellín, Colombia, by Nicéforo María in December 1919 and January 1920.

DISTRIBUTION: All referred specimens of *Handleyomys intectus* are from the central Andes (Cordillera Central) of Colombia between 1500 and 2800 m above sea level in the departments of Antioquia, Quindío, and Risaralda.

EMENDED DIAGNOSIS: A species of *Handleyomys* distinguished by hindfeet that are usually covered dorsally by pure-white (or indistinctly pigmented) hairs; nasals that usually extend posteriorly well beyond the pre-

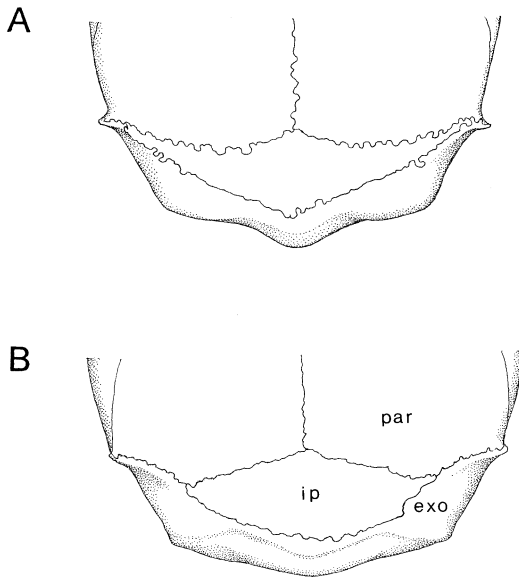


Fig. 15. Typical morphology of the occipital region in *Handleyomys fuscatus* (A, ICN 12703) and *H. intectus* (B, ICN 16079). In *H. intectus*, the interparietal (ip) is narrow (transverse dimension) relative to its depth (antero-posterior dimension), and the flanking sutures between the parietal (par) and exoccipital (exo) are extensive. By contrast, the interparietal of *H. fuscatus* is broad relative to its depth, and the parietal-exoccipital sutures are correspondingly shorter.

maxillary-maxillary suture; incisive foramina that usually have smoothly tapering (never abruptly constricted) lateral margins; and narrow-deep interparietals.

VARIATION: Available samples of *Handleyomys intectus* are remarkably similar throughout the known range of the species, with measurement means that seldom differ geographically by more than about 0.1 mm (table 7). The only noteworthy exception to this tendency are the interparietals of specimens from Quindío and eastern Risaralda, which are markedly narrower, on average, than those of specimens collected in Antioquia. Two specimens collected near El Retiro (ICN 16091, 16093) in the department of Antioquia are unusually small but do not appear to be exceptional in other respects.

SPECIMENS EXAMINED: *Antioquia*, Finca Cañaveral (ICN 16091–16095), La Ceja (AMNH 61575; MLS 187vii, 188vii), La Forzosa (ICN 16073–16079), Río Negro

TABLE 4
Composition of Geographic Samples Used to Calculate Mahalanobis Distances

Samples ^a	Localities ^b	N ^c
Western Andes		
Western Risaralda	9–11, 13–15	40
Valle del Cauca	16–20	6
Central Andes		
Northern Antioquia	1, 6	11
Southern Antioquia	2, 4, 5	7
Quindío & eastern Risaralda	7, 8, 12	16

^a Samples are listed from north to south within each cordillera.

^b Numbered localities are mapped in figure 12 and described in the gazetteer (appendix).

^c Sample size: number of adult specimens with complete craniodental measurement data from which Mahalanobis distances were computed. No completely measurable skulls were available from locality 3 (in southern Antioquia).

(FMNH 70296–70306), Santa Elena (BMNH 21.7.1.17–21.7.1.19 [the type series], AMNH 37734), Ventanas (FMNH 70332–70338); *Quindío*, El Roble (AMNH 32928, 32931–32933, 32937, 32940, 33021), Salento (AMNH 32939); *Risaralda*, La Suiza (ICN 12104, 12158–12179, 12891).

NATURAL HISTORY AND BIOGEOGRAPHY

The predominant type of natural vegetation in the Colombian Andes between 1500 and 2800 m above sea level—the known elevational range of *Handleyomys*—is cloud forest,⁷ but anthropogenic habitats (secondary growth, croplands, pastures) are also widespread at these elevations, and xeromorphic formations (dry forests) can occur on rain-shadowed slopes. Explicit descriptions of macro- and microhabitats where

⁷ We use the nontechnical term “cloud forest” for montane rain forests generally, including the formations that Grubb (1977) usefully defined as Lower Montane Rain Forest, Upper Montane Rain Forest, and Subalpine Rain Forest. Nevertheless, we cite other synonyms used by Colombian advocates of Holdridge’s (1947) life-zone nomenclature because these are widely used and published maps are available (Espinal and Montenegro, 1963). For a critical review of “cloud forest” and its technical synonyms from a field zoologist’s point of view, see Myers (1969); for another (botanical) perspective, see Webster (1995).

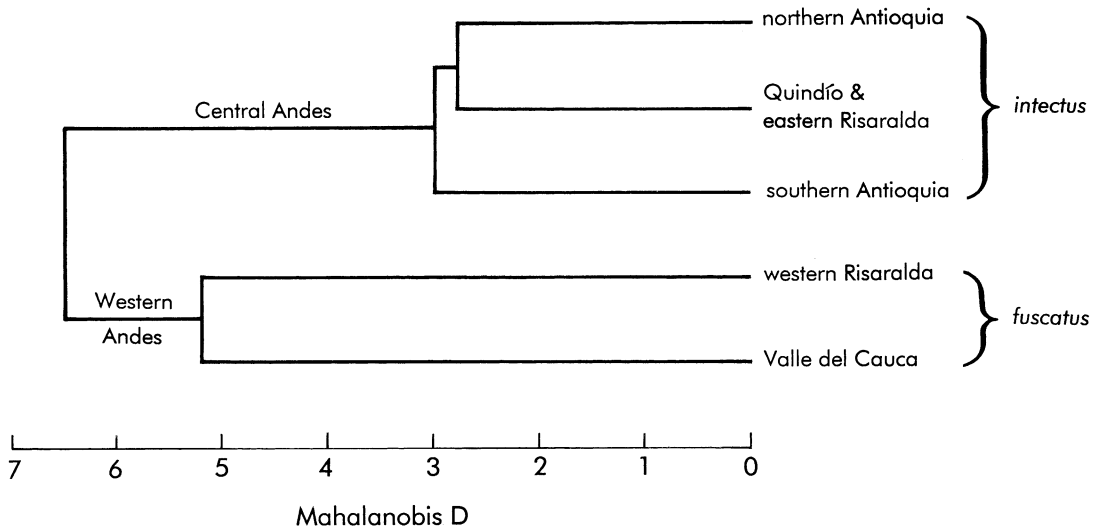


Fig. 16. Results of UPGMA clustering of Mahalanobis distances (D) among five geographic samples of *Handleyomys* defined in table 4. The samples labeled “northern Antioquia”, “Quindío & eastern Risaralda”, and “southern Antioquia” are in the central Andes (Cordillera Central) and correspond to the species we recognize as *H. intectus*. The groups labelled “western Risaralda” and “Valle del Cauca” are in the western Andes (Cordillera Occidental) and correspond to the species we recognize as *H. fuscatus*.

TABLE 5
Principal Components Analysis of Craniodental Measurement Variation Among Adult *Handleyomys* from La Suiza and El Campamento^a

	Unit eigenvectors	
	PC1	PC2
Coefficients:		
CIL	0.109	0.259
LD	0.160	0.356
LM	-0.087	0.110
BM1	0.031	0.196
LIF	0.413	0.182
BIF	0.113	0.065
BPB	0.164	0.484
BZP	-0.233	0.511
LIB	0.082	0.032
ZB	0.162	0.203
NL	0.237	0.302
IPB	-0.775	0.299
% Variance	47.7	26.8

^a Principal components were extracted from the variance-covariance matrix of measurements transformed to their natural logarithms. Specimen scores (N = 16 for La Suiza, N = 21 for El Campamento) are plotted in figure 17.

specimens were captured are therefore important for determining the ecological circumstances in which small Andean mammals actually occur. Because such descriptions are not available for most historical collecting localities (e.g., figs. 18, 19), the following accounts provide ecological information from several sites where *Handleyomys* has recently been taken by Colombian researchers. These data, together with additional information summarized in the appendix, provide the basis for subsequent generalizations about the ecogeographic distribution of *Handleyomys*.

HABITAT DESCRIPTIONS

Departamento Antioquia, Municipio Anorí (9 km S Anorí), Vereda Roble Arriba, bosque La Forzosa, 1775 m: The protected area known as La Forzosa (fig. 12: locality 1) is a ca. 450 ha fragment of primary premontane wet forest (“bosque muy húmedo Subtropical” of Espinal and Montenegro, 1963) on the northeastern flanks of

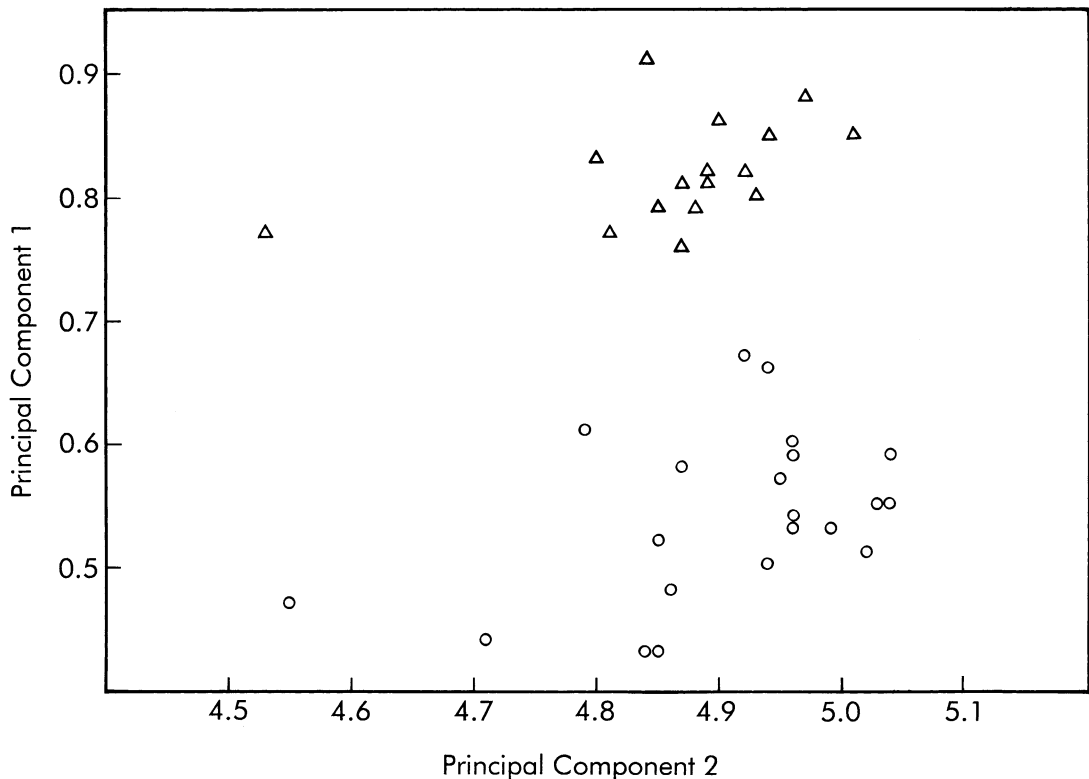


Fig. 17. Specimen scores of *Handleyomys intectus* (open triangles, from La Suiza [locality 12]) and *H. fuscatus* (open circles, from El Campamento [locality 14]) on the first two principal components extracted from the variance-covariance matrix of log-transformed craniodental measurements (see text). Variable coefficients and eigenvalues (scaled as percentages of the total variance) are provided in table 5.

the central Andes east of the upper Río Nechí (Cuervo et al., 2001). Frequent mists, high annual precipitation (2600–3500 mm), and high relative humidity (77–95%) characterize the local climate, which includes a short dry season from December to February and a longer wet season from May to October (op. cit.). The local topography is complex,

... dissected by steep river valleys and gorges. Primary forests are characterized by a heterogeneous canopy, from 6–7 m on the ridges, 15–17 m on the slopes, increasing to 20 m along watercourses, with occasional emergent trees up to 30 m. Understorey cover is densest on the steep slopes, dominated by terrestrial herbaceous plants and by epiphytes on ridges. The forests are particularly dynamic, with a high natural treefall rate and landslides caused by high precipitation on steep slopes with shallow soils. (Cuervo et al., 2001: 361)

Carlos A. Delgado V. collected seven specimens of *Handleyomys intectus* at this site between 7 and 11 January 2001. The an-

imals were taken in Sherman live traps set in mature forest festooned with bromeliads, ferns, moss, and orchids; no specimens were taken in traps set along the forest edge or in clearings. Traps that took *H. intectus* at La Forzosa were placed on the ground among the elevated roots of palms and other trees, beneath the large leaves of low-growing understorey plants, and inside rotting logs. All captured individuals apparently entered the traps at night. Sympatric rodents trapped at the same locality included *Heteromys australis* (voucher: ICN 16072), *Rhipidomys latimanus* (ICN 16087, 16088), *Oryzomys albigularis* (ICN 16084–16086), and *Melanomys caliginosus* (ICN 16080–16083).

Departamento Antioquia, Municipio El Retiro (4 km S El Retiro), Vereda Puente Peláez, Finca Cañaveral, 2100 m: Perched on the western flanks of the central Andes in the valley of the Río La Miel, the landscape

TABLE 6
Summary Statistics^a for External and Craniodental Measurements (in millimeters)
and Weights (in grams) of Adult *Handleyomys fuscatus*

	Valle del Cauca ^b	W Risaralda ^c
HL	105 ± 10 (93–130) 14	96 ± 6 (80–108) 47
LT	94 ± 11 (75–110) 14	90 ± 6 (77–108) 47
HF	24 ± 1 (22–26) 15	24 ± 1 (22–25) 51
Ear	15 (15–16) 3	14 ± 1 (10–17) 51
CIL	24.5 ± 0.7 (23.1–25.8) 11	23.7 ± 0.7 (21.6–25.7) 51
LD	7.4 ± 0.5 (6.3–8.3) 15	7.0 ± 0.3 (6.1–7.6) 51
LM	4.3 ± 0.1 (4.0–4.5) 15	4.3 ± 0.1 (4.0–4.6) 51
BM1	1.3 ± 0.1 (1.2–1.4) 15	1.3 ± 0.1 (1.2–1.4) 51
LIF	4.0 ± 0.2 (3.4–4.4) 15	4.2 ± 0.3 (3.7–4.8) 51
BIF	1.9 ± 0.1 (1.7–2.1) 14	2.0 ± 0.2 (1.8–2.8) 51
BPB	2.8 ± 0.2 (2.5–3.2) 14	2.7 ± 0.2 (2.2–3.1) 50
BZP	2.2 ± 0.2 (1.9–2.5) 15	2.4 ± 0.2 (2.2–2.8) 51
LIB	5.0 ± 0.2 (4.8–5.3) 15	4.8 ± 0.1 (4.5–5.2) 51
ZB	14.3 ± 0.6 (13.6–15.3) 10	13.7 ± 0.5 (12.6–14.8) 42
NL	10.4 ± 0.6 (8.9–11.5) 14	10.5 ± 0.5 (9.1–11.5) 50
IPB	9.4 ± 0.4 (8.5–9.8) 11	9.2 ± 0.5 (8.2–10.2) 51
Weight	26 (24–31) 4	25 ± 4 (19–34) 49

^a The mean plus or minus one standard deviation (for samples with $N \geq 10$), the observed range (in parentheses), and the sample size.

^b Included specimens are from localities 16–20 in Departamento Valle del Cauca (see fig. 12, appendix): AMNH 32227–32233, 32237; ICN 4376, 4388, 6903; IND-M 3659; USNM 507267–507269.

^c Included specimens are from localities 9–11 and 13–15 in western Departamento Risaralda (see fig. 12, appendix): ICN 12208, 12701–12704, 12706–12710, 12725–12727, 12783–12786, 12788–12791, 12794, 12796–12803, 12806–12817, 12819–12827.

of Finca Cañaveral (fig. 12: locality 2) is dominated by anthropogenic habitats, principally pastures (for milk cattle) and agricultural fields, but relictual forest (“bosque húmedo Subtropical” according to Espinal and Montenegro’s [1963] map) survives along the margins of streams that descend from continuous forest on steeper slopes above the valley floor. Carlos A. Delgado V. collected three specimens of *Handleyomys intectus* on two brief visits to this site, once in August 2000 and again in March 2001. The animals were trapped at night in dense forest (including *Cecropia* sp., *Quercus humboldti*, *Inga* sp., *Schefflera* sp., *Guatteria goudotiana*, *Vismia* sp., Piperaceae, Rubiaceae, ferns, orchids, and bromeliads) along the banks of a small unnamed tributary of the Río La Miel. Other rodents taken in the same traplines as *Handleyomys* at this site were *Akodon affinis* (vouchers: ICN 16089, 16090), *Microryzomys minutus* (ICN 16096), and *Reithrodontomys mexicanus* (ICN 16097–16100).

Departamento Risaralda, Municipio Pereira, Corregimiento La Florida, Vereda

La Suiza, 1900–1950 m: The area known as La Suiza (fig. 12: locality 12) is a protected area in the valley of the Río Otún on the western slope of the Cordillera Central. Although the biological station at La Suiza is surrounded by pastures, agricultural fields, and alder (*Alnus acuminata*) plantations, some primary cloud forest (“bosque muy húmedo Montano Bajo” of Espinal and Montenegro, 1963; including large specimens of *Quercus humboldti*) persists along the nearby Quebrada La Hacienda and on surrounding hillsides. Local rainfall is bimodally distributed, with average monthly maxima in June (237 mm) and November (290 mm); January is the driest month on average (121 mm), and the mean annual total is 2038 mm (Aguilar and Rangel, 1994). The median annual temperature is about 24°C, with average daily maxima and minima of 33° and 16°, respectively (op. cit.).

The small mammal fauna at La Suiza was sampled by ICN researchers on two separate occasions in 1992. On the first visit to this site, MGL and Angélica Peñuela trapped for

TABLE 7
Summary Statistics^a for External and Craniodental Measurements (in millimeters)
and Weights (in grams) of Adult *Handleyomys intectus*

	Quindío & E Risaralda ^b	S Antioquia ^c	N Antioquia ^d
HBL	103 ± 8 (85–113) 22	101 ± 7 (88–114) 12	99 ± 6 (88–112) 13
LT	94 ± 7 (78–106) 22	94 ± 9 (75–106) 12	97 ± 4 (90–102) 13
HF	24 ± 1 (22–26) 22	23 ± 1 (21–25) 15	25 ± 1 (23–26) 13
Ear	13 ± 2 (10–16) 18	15 ± 1 (13–16) 12	15 ± 1 (14–17) 13
CIL	24.0 ± 0.9 (21.6–24.8) 20	23.3 ± 1.3 (21.0–24.7) 11	24.3 ± 0.9 (22.0–25.5) 13
LD	7.1 ± 0.4 (6.2–7.7) 23	7.1 ± 0.6 (5.9–7.9) 14	7.3 ± 0.4 (6.2–7.9) 13
LM	4.1 ± 0.1 (3.8–4.2) 23	4.1 ± 0.2 (3.8–4.4) 15	4.2 ± 0.1 (3.9–4.4) 13
BM1	1.3 ± 0.0 (1.2–1.4) 23	1.3 ± 0.0 (1.2–1.4) 15	1.3 ± 0.0 (1.2–1.4) 13
LIF	4.5 ± 0.2 (4.0–4.8) 23	4.4 ± 0.3 (3.8–4.7) 14	4.6 ± 0.2 (4.2–5.0) 13
BIF	2.0 ± 0.1 (1.8–2.1) 23	1.9 ± 0.1 (1.7–2.0) 14	2.0 ± 0.1 (1.9–2.2) 13
BPB	2.7 ± 0.2 (2.2–2.9) 23	2.7 ± 0.1 (2.5–3.1) 14	2.8 ± 0.1 (2.6–3.0) 13
BZP	2.2 ± 0.2 (1.8–2.4) 23	2.2 ± 0.1 (2.0–2.4) 14	2.4 ± 0.1 (2.1–2.6) 13
LIB	4.9 ± 0.1 (4.6–5.1) 23	4.9 ± 0.2 (4.7–5.3) 15	5.0 ± 0.1 (4.8–5.3) 13
ZB	14.1 ± 0.5 (12.9–14.6) 18	13.8 ± 0.5 (12.8–14.7) 13	14.2 ± 0.5 (13.2–14.9) 11
NL	11.1 ± 0.5 (9.6–11.7) 22	11.1 ± 0.8 (9.5–12.1) 10	11.4 ± 0.8 (9.6–12.5) 13
IPB	7.2 ± 0.5 (6.2–7.8) 22	7.9 ± 0.5 (7.2–8.8) 11	8.0 ± 0.4 (7.4–8.8) 13
Weight	26 ± 5 (17–33) 17	24 (24–25) 2	28 (25–30) 6

^a The mean plus or minus one standard deviation (for samples with N ≥ 10), the observed range (in parentheses), and the sample size.

^b Included specimens are from localities 7 and 8 in Departamento Quindío, and from adjacent locality 12 in eastern Departamento Risaralda (see fig. 12, appendix): AMNH 32931, 32932, 32939, 32940, 33021; ICN 12104, 12158–12161, 12163–12165, 12167–12169, 12171–12174, 12178, 12179, 12891.

^c Included specimens are from localities 2, 4, and 5 in southern Departamento Antioquia (see fig. 12, appendix): AMNH 37734; BMNH 21.7.1.17–21.7.1.19 (holotype and paratypes); FMNH 70297, 70299–70301, 70303–70306; ICN 16091–16093.

^d Included specimens are from localities 1 and 6 in northern Departamento Antioquia (see fig. 12, appendix): FMNH 70332–70338; ICN 16073–16079.

five consecutive nights (22–27 February) in the dry season; on the second, MGL and Rocio Polanco trapped for another five consecutive nights (8–13 June) in the rainy season. The equipment used on both visits consisted of medium-size (ca. 80 × 90 × 230 mm) Sherman live traps, large (ca. 100 × 115 × 380 mm) Sherman live traps, and small snap traps (Museum Specials), all of which were placed on the ground and similarly baited. Traplines were located along the margins of forest clearings, along narrow trails through the forest, and along the banks of Quebrada La Hacienda. Altogether, these faunal-sampling efforts amounted to 1163 trap-nights, of which 603 were in February and 560 in June. *Handleyomys intectus* was the most commonly trapped species at La Suiza on both visits, accounting for 50% of total captures (table 8). All trapped animals were re-

covered at dawn and appeared to have been captured during the previous night.

Departamento Risaralda, Municipio Pueblo Rico, Vereda Siató, 1520–1620 m:

The steep-sided western foothills of the Cordillera Occidental near Pueblo Rico (fig. 12: locality 13) have been largely cleared for agriculture and animal husbandry, but fragments of cloud-forest vegetation (“bosque muy húmedo Montano Bajo” of Espinal and Montenegro, 1963) persist along the margins of local streams. Quantitative climatic data are unavailable, but local precipitation is bimodally distributed with maxima in April–June and October–November and minima in January and July. The local fauna of small mammals was sampled in the valley of the Río Siató (several kilometers SE Pueblo Rico), where MGL and 33 undergraduate students from the Universidad Nacional set



Fig. 18. Cloud forest at San Antonio, Departamento Valle del Cauca, Colombia. The holotype and 11 paratypes of *Handleyomys fuscatus* were collected near San Antonio by William B. Richardson, a professional collector employed by the 1911 AMNH expedition to Colombia. Richardson's skin labels record local captures of *H. fuscatus* at elevations ranging from 7000 to 8000 ft (ca. 2130–2440 m), but provide no additional ecological details. Although other habitats were present near San Antonio, most of the collecting efforts by AMNH staff at this locality were focused on the forest (see Chapman, 1917: 24), which is indicated as “bosque pluvial Montano Bajo” on Espinal and Montenegro's (1963) vege-

medium-size Sherman live traps, National wire live traps (ca. 145 × 145 × 410 mm), and Museum Specials along the forested banks of the Quebrada La Cristalina for eight nights (20–29 September) in the late-dry/early-wet season of 1991. All traps were set on the ground. A total of 21 captures were recorded in 405 trap-nights, including 4 specimens of *Handleyomys fuscatus*, 10 *Akodon affinis* (vouchers: ICN 12765–12767), 4 *Oryzomys albigularis* (ICN 12715, 12716, 12719), 2 *Melanomys caliginosus* (ICN 12717), and 1 *Oligoryzomys fulvescens* (ICN 12718). All trapped animals were encountered at dawn and were assumed to have been captured during the previous night.

Departamento Risaralda, Municipio Santuario, Vereda El Campamento, 2400–2500 m: This locality on the eastern slope of the Cordillera Occidental (fig. 12: locality 14) is characterized by steep terrain with patches of disturbed (selectively logged) primary cloud forest (“bosque muy húmedo Subtropical” of Espinal and Montenegro, 1963), agricultural fields, and pastures (fig. 2). The local climate is presumably similar to that described by Sánchez-Páez et al. (1991) from the nearby Parque Nacional Natural Tatamá (see Los Planes, below). ICN researchers Pedro Sánchez Palomino and Marcela Morales trapped small mammals at El Campamento on six nights (19–24 and 26 November) during the rainy season of 1991. All traps (medium-size Shermans and Museum Specials) were set on the ground inside the forest fragments. Seventy traps were set each night, for a total of 420 trap-nights. *Handleyomys fuscatus* was the most abundant of seven species taken at this locality, accounting for about 47% of all recorded captures. In order of decreasing capture frequency, the other taxa trapped at El Campamento were *Oryzomys albigularis* (vouchers: ICN 12001–12023, 12616, 12617), *Microoryzomys minutus* (ICN 12720–12722),

Akodon affinis (ICN 12614, 12615), *Reithrodontomys mexicanus* (ICN 12723), *Thomomys cinereiventer* (ICN 12623), and *T. aureus* (unvouchered).

Departamento Risaralda, Municipio Santuario, Vereda Los Planes, 2530 m: The eastern slopes of the Cordillera Occidental from the municipal capital of Santuario (ca. 1500 m) to the vicinity of Los Planes (fig. 12: locality 15) have been almost completely deforested for agriculture and animal husbandry, with only fragments of natural vegetation remaining along watercourses. Above 2500 m, however, is an extensive landscape of primary cloud forest (“bosque muy húmedo Montano Bajo” of Espinal and Montenegro, 1963) that is protected by the Parque Nacional Natural Tatamá. The ICN base camp at Los Planes was an abandoned shelter about an hour and a half by mule from finca Las Delicias (ca. 2100 m) via a dirt road that parallels the Río San Rafael. Collections were made just inside the park boundary, about 500 m above the south bank of the river, in a zone of transition between the denuded lower slopes and the primary forest. The eastern slopes of Tatamá are said to have a median annual temperature of about 17°C and an annual precipitation of 2000–2800 mm; precipitation is bimodal, with maxima in May and October–November and minima in February and July (Sánchez-Páez et al., 1991).

Small mammals were trapped at Los Planes on eight consecutive nights (27 October to 4 November) in the rainy season of 1991 by an ICN team consisting of Pedro Sánchez Palomino, MGL, and Yaneth Muñoz-Saba. All of the traps (medium-size Shermans and Museum Specials) were set on the ground in low, shrubby secondary vegetation that was said to be about five years old by local inhabitants; primary forest, however, occurs in close proximity, and some traps were set along the forest edge. *Handleyomys*

←

tation map. High humidity and cool temperatures are reliably indicated by the profusion of vascular epiphytes and hemiepiphytes (aroids, bromeliads, ferns) and moss that cover tree trunks and limbs in this view and in the accompanying close-up (fig. 19). Essentially similar environments have been described by most modern collectors of *Handleyomys* (see text). Photographed in May 1911 by F.M. Chapman.



Fig. 19. Close-up of cloud-forest vegetation at San Antonio (see preceding figure caption for eco-geographic details). A local boy (standing just left of center) provides a sense of scale. Clearly shown is the lush vegetation (dominated by large monocots in this view) at ground level, where all specimens of *Handleyomys* accompanied by microhabitat information have been trapped at other localities. Photographed by in May 1911 by F.M. Chapman.

TABLE 8

Small Mammal Trapping Results at La Suiza
(Table entries are numbers of captures.)

	Visit 1	Visit 2	Totals
<i>Handleyomys intectus</i> ^a	11	12	23
<i>Oryzomys albigularis</i> ^b	5	8	13
<i>Akodon affinis</i> ^c	3	3	6
<i>Heteromys australis</i> ^d	1		1
<i>Sigmodontomys alfari</i> ^e	1		1
<i>Oryzomys alfaroi</i> ^f		1	1
Unidentified didelphid ^g	1		1
Totals	22	24	46

^a Identified as *Oryzomys* sp. by Gómez-Laverde (1994). Voucher material is listed elsewhere in this report.

^b Vouchers: ICN 12119–12123, 12126–12132, 12180.

^c Vouchers: ICN 12105–12107, 12114–12116.

^d Voucher: ICN 12103.

^e Identified as *Oryzomys alfari* by Gómez-Laverde (1994). Voucher: ICN 12157.

^f Voucher: ICN 12188.

^g A species of *Marmosa* (sensu lato); not examined by RSV. Voucher: ICN 12102.

fuscatus was the third most-abundant species taken in 460 trap-nights at Los Planes, where it comprised about 22% of all recorded captures (table 9). All trapped animals were recovered at dawn and were assumed to have been captured during the previous night.

SUMMARY

Available habitat descriptions and trapping records indicate that species of *Handleyomys* occur in both primary cloud forests and adjacent anthropogenic vegetation (secondary growth). Although climatic data are rarely available from the exact sites where specimens have been collected, plotting collection localities on published ecological maps suggests that *Handleyomys* is most frequently encountered in relatively cool and very humid environments (12–18°C mean ambient temperature; >2000 mm annual precipitation), corresponding to the vegetation zone that Espinal and Montenegro (1963) designate as “bosque muy húmedo Montano Bajo” (table 10). In the classification of tropical montane forest vegetation suggested by Grubb (1977), the natural habitat at most *Handleyomys* collection localities would be called Lower Montane Rain Forest, but specimens have also been taken in habitats cor-

responding to Upper Montane Rain Forest in his system. In Chapman's (1917: 84–93) classification of Colombian life zones, *Handleyomys* is a member of the humid-Subtropical and humid-Temperate faunas.

All of the other sympatric small mammals that have been collected with *Handleyomys* are likewise known primarily from wet forests. Whereas some are commonly encountered in foothill landscapes (e.g., *Heteromys australis*, *Melanomys caliginosus*, *Sigmodontomys alfari*), others are typically found at middle elevations (e.g., *Oryzomys albigularis*), and a few are genuinely upper-montane taxa (e.g., *Caenolestes fuliginosus*, *Thomasomys* spp.). Conspicuously absent from all known sites where *Handleyomys* have been collected are any small mammals primarily associated with lowland forests (e.g., *Proechimys* spp.) or with semiarid habitats (e.g., *Sigmodon hispidus*, *Zygodontomys brevicauda*).

Available trapping records suggest that *Handleyomys* is predominantly terrestrial and nocturnal, but these data are less than conclusive because traps were not simultaneously set in trees, and because trapped animals encountered at dawn might have been caught before dark the previous day. However, terrestrial habits are consistent with inferences based on morphology: the long-narrow hindfoot of *Handleyomys* (with short, nonopposable outer digits; fig. 3) resembles the condition seen in many other murids with better-documented terrestrial behavior (e.g., Amazonian species of *Oryzomys*; see Malcolm [1991], Patton et al. [2000], and Voss et al. [2001] for relevant trapping data). By contrast, semiarboreal and arboreal muroids typically have shorter, broader hindfeet with longer outer digits, of which dV is often semiopposable (Voss et al., 2001: fig. 53B, C). The relatively short, naked-appearing tail of *Handleyomys* is another indication of terrestrial locomotion because arboreal murids usually have relatively longer tails with longer, coarser hairs that sometimes form a terminal tuft (Voss et al., 2001: fig. 61). Lastly, the dull, drab pelage of *Handleyomys* is similar to that of many other nocturnal montane murids and contrasts with the more richly pigmented fur of some taxa that are known to be active in the daytime (e.g., *Scotinomys*,

TABLE 9
Small Mammal Trapping Results at Los Planes
 (Table entries are numbers of captures.)

	Trapping nights ^a								Totals
	1	2	3	4	5	6	7	8	
<i>Oryzomys albigularis</i> ^b	9	3		3	5	5	1	2	28
<i>Akodon affinis</i> ^c	3	2	2	6	4				17
<i>Handleyomys fuscatus</i> ^d	4	1	4	1	2	3	1		16
<i>Caenolestes fuliginosus</i> ^e	1	2	1			1			5
<i>Thomasomys cinereiventer</i> ^f	1	1			1	1			4
<i>Reithrodontomys mexicanus</i> ^g						1	1		2
<i>Thomasomys aureus</i> ^h	1								1
Totals	19	9	7	10	12	11	3	2	73

^aFrom 27 October to 4 November 1991 (see text). Seventy traps were set on nights 1–4, 75 traps on nights 5 and 6, and 15 traps on nights 7 and 8.

^bVouchers: ICN 11972–11997, 12617, 12618.

^cVouchers: ICN 12597–12613.

^dVouchers are listed elsewhere in this report.

^eA sixth specimen was captured by hand. Vouchers: ICN 11966–11971.

^fVouchers: ICN 12619–12622.

^gVouchers: ICN 11998–11999.

^hVoucher: ICN 12724.

Melanomys; Hooper and Carleton [1976], Gardner [1983]).

Other aspects of the natural history of *Handleyomys* are obscure. No noteworthy dietary information is available; only a few ectoparasite records have been published (Brennan, 1968); nesting sites, litter sizes, and gestation lengths are unknown; and data from year-long trapping programs are not available to assess reproductive seasonality. Obviously, the absence of concrete information about so many biological details provides considerable scope for productive future fieldwork on these animals.

DISCUSSION

All of the 20 known collecting localities of *Handleyomys* are above 1500 m in the western and central Andes of Colombia (fig. 12, appendix), but whether or not these records provide a reliable indication of the true geographic range of the genus remains to be considered. Because most Neotropical landscapes are still poorly inventoried for small mammals, distinguishing patterns of endemism from collecting artifacts is a significant research problem. However, some inferences about probable range limits can be made.

Unlike certain notoriously elusive Neotropical mammals that can only be collected in special microhabitats (e.g., ichthyomyines: Stirton, 1944; Voss, 1988), species of *Handleyomys* appear to be abundant (or at least easily trapped) at most places where they have been found to date. Therefore, the absence of specimens from large collections obtained by general trapping programs can be taken as a plausible indication that the genus does not occur in the region(s) where such collections were made. It is not likely, for example, that *Handleyomys* occurs in the cloud-forested mountains along the Panamanian frontier (Serranía de Pirre, Serranía del Darién), because these highlands have been repeatedly visited by mammalogical collectors (Anthony, 1916; Goldman, 1920; Pearson, 1939; Handley, 1966, 1972). Similarly, sizable collections have accumulated over the years from many forested (or formerly forested) localities surrounding Bogotá in the eastern Andes (Cordillera Oriental) of Colombia (material that we examined is in the AMNH, BMNH, FMNH, IAvH, ICN, MLS, and USNM), and from the vicinity of Quito in the Andes of northern Ecuador (representative material examined is in the

TABLE 10
Summary Characteristics of *Handleyomys* Habitats Inferred from Ecological Maps

Vegetation ^a	Number of localities ^b	Average temperature ^c	Annual precipitation ^c
bh-ST	1	18–24°C	1000–2000 mm
bmh-ST	2	17–24°C	2000–4000 mm
bp-ST	1	17–24°C	>4000 mm
bh-MB	1	>12°C	1000–2000 mm
bmh-MB	10	12–18°C	2000–4000 mm
bp-MB	3	12–18°C	>4000 mm
bmh-M	1	6–12°C	1000–2000 mm
bp-M	1?	6–12°C	>2000 mm

^aAbbreviations: bh-ST, bosque húmedo Subtropical; bmh-ST, bosque muy húmedo Subtropical; bp-ST, bosque pluvial Subtropical; bh-MB, bosque húmedo Montano Bajo; bmh-MB, bosque muy húmedo Montano Bajo; bp-MB, bosque pluvial Montano Bajo; bmh-M, bosque muy húmedo Montano; bp-M, bosque pluvial Montano.

^bNumber of gazetteer entries with inferred vegetation type (see appendix).

^cFrom Espinal and Montenegro (1963).

AMNH, BMNH, and UMMZ). The Sierra Nevada de Santa Marta (on the Caribbean coast of Colombia, north of the frame of reference depicted in fig. 12) was the focus of intensive general collecting in the late 19th and early 20th centuries (Bangs, 1900; Allen, 1904), and the Cordillera de Mérida (in western Venezuela) is mammalogically familiar territory (Handley, 1976; Péfaur and Díaz de Pascual, 1985; Durant and Díaz, 1995; Soriano et al., 1999a, 1999b). The absence of *Handleyomys* from all of these relatively well-sampled areas is compelling evidence that the genus is not widely distributed across the mountainous landscapes of northwestern South America.

Collections from various other localities suggest that species of *Handleyomys* might not be widely distributed even in the mountain systems where they are known to occur. Thus, *H. fuscatus* is notably absent among the FMNH material collected by Philip Hershkovitz at Santa Bárbara (6°25'N, 76°00'W) and other sites in the northern part of the western Andes, nor does it occur in Kjell von Sneider's collections (also at FMNH) from the vicinity of Cerro Munchique (ca. 2°32'N, 76°57'W) in the southern part of the same cordillera. *Handleyomys inexpectatus* is likewise absent from FMNH collections made by Philip Hershkovitz near San Antonio (1°57'N, 76°29'W) and San Agustín (1°53'N, 76°16'W) in the southern part of the central Andes. In fact, specimens of *Handley-*

omys are unknown from dozens of other localities in the western and central cordilleras that have been trapped (albeit briefly) by various mammalogical collectors throughout the 1900s. Although these negative results might be overturned by more intensive faunal sampling at some future date, they all tend to support the prima facie conclusion from known records of positive occurrence that *H. fuscatus* might be narrowly endemic to the central part of the western Andes and *H. inexpectatus* to the northern part of the central Andes.

We are not aware of any other mammalian clade that consists of one species restricted to the western cordillera and the other to the central cordillera, nor is any mammalian taxon currently known to be endemic to just these two (western + central) mountain ranges. However, the apparent absence of any mammals with the same distribution as *Handleyomys* is not surprising because there has been almost no revisionary taxonomic research to date on northern Andean mammals (see below). Although several such studies are now in progress, only nonmammalian vertebrate distributions are currently available for biogeographic comparisons.

Recent progress in alpha-taxonomic research on the rich amphibian fauna of Colombia, for example, has documented relevant distributional patterns. In his analysis of speciation phenomena in the leptodactylid frog genus *Eleutherodactylus*, Lynch (1999a)

identified five sister-species pairs (*albericoi-lichenoides*, *deinops-torrenticola*, *juanchoi-helvolus*, *ptochus-suetus*, *ruizi-necopinus*), each consisting of one member endemic to the western Andes and the other to the central Andes. In all but one of these pairs, both sister species inhabit essentially the same habitat (cloud forest at middle elevations, ca. 1800–2700 m) as *Handleyomys*, and the disjunct areas of endemism they occupy (in the central part of the western cordillera and the northern part of the central cordillera) correspond closely to the known distributions of *H. fuscatus* and *H. intectus* (op. cit.: fig. 26).

Another array of montane amphibian species are western + central Andean endemics with disjunct distributions separated by the valley of the Río Cauca. This fauna includes three cloud-forest centrolenids (*Centrolene grandisonae*, *Cochranella ruizi*, *C. savagei*), three cloud-forest dendrobatids (*Colostethus abditaurantius*, *Minyobates bombetes*, *M. opisthomelas*), one cloud-forest hylid (*Hyla columbiana*), nine cloud-forest leptodactylids (*Eleutherodactylus brevifrons*, *E. boulengeri*, *E. cabrerai*, *E. erythroleura*, *E. gracilis*, *E. mantipus*, *E. palmeri*, *E. permixtus*, *E. thecopternus*), and two gymnophionans (*Caecilia occidentalis*, *C. orientalis*). However, each of these amphibian species is more widely distributed within the western and/or central Andes than *Handleyomys*; none is restricted to just the central part of the western Andes plus the northern part of the central Andes (Ruiz-Carranza et al., 1996; Lynch and Rueda-Almonacid, 1997; Lynch et al., 1997; Lynch, 1998, 1999b).

Birds are the only other Colombian vertebrate group for which a comprehensive source of distributional data is available, but few avian taxa appear to be as narrowly endemic as *Handleyomys* and the amphibians mentioned above. To the best of our knowledge, ornithologists have not identified any sister-species pairs of cloud-forest birds of which one member is endemic to the western Andes and the other to the central Andes, nor are many avian species endemic to just those cordilleras. Indeed, only 2 of the 1475 Colombian bird species mapped by Hilty and Brown (1986) are western + central Andean endemics with disjunct cloud-forest distributions separated by the Río Cauca valley

(*Chlorochrysa nitidissima*, *Bangsia melanochlamys*).

Although the absence of compelling evidence for western + central Andean endemism in the avian data suggests that distributional patterns in cloud-forest birds might differ significantly from those of sympatric nonvolant vertebrates, the continuing discovery of new taxa (e.g., Cuervo et al., 2001) underscores our still-incomplete knowledge of the Colombian avifauna. Additionally, the possibility that much relevant distributional data might be concealed among the numerous avian “subspecies” discussed (but not mapped) by Hilty and Brown (1986) merits careful evaluation in any comprehensive future study of cloud-forest vertebrate endemism in northwestern South America.

Because no simple scenario of vicariance or dispersal seems likely to account for the documented complexity of Colombian montane vertebrate biogeography (Chapman, 1917, 1926; Müller, 1973; Haffer, 1974; Duellman, 1979; Cracraft, 1985; Lynch et al., 1997), it seems premature to speculate about historical explanations for the congruent distributions of *Handleyomys* and a few clades of eleutherodactyline frogs. Possibly, some paleoecological connection between cloud-forest habitats in the central part of the western Andes and those in the northern part of the central Andes might be discovered by palynological sampling in the Río Cauca valley. A more compelling research goal for systematic mammalogists, however, is to evaluate the generality of the biogeographic pattern described above. Is *Handleyomys* the only mammalian clade with this distribution, or can others be identified among the several genera and species complexes of sympatric small mammals that remain to be revised taxonomically? Future systematic research on such neglected taxa as *Akodon*, *Thomasomys*, and the *Oryzomys albigularis* group may provide answers to this and other outstanding questions about mammalian endemism in the Colombian Andes.

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APPENDIX: Gazetteer

We examined specimens of *Handleyomys* from 20 localities in the western Andes (Cordillera Occidental) and central Andes (Cordillera Central) of Colombia. Numbers preceding each entry in the list that follows are keyed to symbols on the accompanying map (fig. 12). Italic type identifies Colombian departments, and boldface identifies locality names as cited in the text of this report. Geographic coordinates, seldom recorded by fieldworkers, were obtained from various published sources, including departmental topographic maps published by the Instituto Geográfico

“Agustín Codazzi” (Bogotá), gazetteers (DMA, 1988; Paynter, 1997), and other compilations of specimen data (e.g., Anderson, 1999). Following a semicolon, we provide the name(s) of the collector(s) and the date(s) on which specimens were collected (in parentheses). For localities lacking explicit descriptions of capture habitats (as summarized in the preceding text), inferences about local vegetation were based on Espinal and Montenegro’s (1963) ecological map of Colombia (from which relevant descriptors are quoted verbatim; e.g., “bosque muy húmedo Montano

Bajo”), taking into account geographical coordinates and known elevations of collected material.

1. *Antioquia*, Municipio Anorí (9 km S Anorí), Vereda Roble Arriba, bosque **La Forzosa**, 6°59'N, 75°08'W [on W slope of central Andes], 1775 m; Carlos A. Delgado V. (7–11 January 2001). See text for a description of local habitats.
2. *Antioquia*, Municipio El Retiro (4 km S El Retiro), Vereda Puente Peláez, **Finca Cañaverale**, 6°01'N, 75°30'W [on E slope of central Andes], 2100 m; Carlos A. Delgado V. (11 August 2000, 14 March 2001). See text for a description of local habitats.
3. *Antioquia*, [Municipio La Ceja], **La Ceja** [6°02'N, 75°26'W, on E slope of central Andes at 2217 m]; Nicéforo María (1919, 1921). Natural vegetation probably “bosque húmedo Montano Bajo”.
4. *Antioquia*, [Municipio Medellín], **Santa Elena** [ca. 6°13'N, 75°32'W; in central Andes], 9000 ft [2743 m]; Howarth S. Boyle (19 November 1911), Nicéforo María (December 1919–January 1920). The exact provenance of Boyle’s and Nicéforo María’s material from Santa Elena, which is said to be near Medellín (Chapman, 1917; Thomas, 1921), is uncertain because several localities near the city are named Santa Elena or Santa Helena (phonetically equivalent names in Spanish). Fortunately, all of them fall within a small region, approximately 9 × 9 km, that can be represented by a single point on our map (fig. 12). The best match with Boyle’s recorded elevation (Nicéforo María did not record this datum) corresponds to the above coordinates on IGAC’s (1979) 1:25,000 topographic sheet. Paynter’s (1997) longitude for Santa Elena (71°10'W) is an obvious mistake. Natural vegetation at ca. 2700 m probably “bosque muy húmedo Montano”.
5. *Antioquia*, [Municipio] Sonsón, 9–15 km E **Río Negrillo** [5°42'N, 75°10'–75°13'W; on W slope of central Andes], 1700–2100 m; Philip Hershkovitz (4–19 October 1950). Natural vegetation probably “bosque muy húmedo Montano Bajo”. According to Dr. Robert P. Anderson (personal commun.), it is likely that Hershkovitz’s specimen labels from this locality refer to measured distances from the municipal center (Sonsón) along the Río Negrillo, rather than to distances from the river as implied by his syntax.
6. *Antioquia*, [Municipio] Valdivia, **Ventanas** [7°05'N, 75°27'W; on NW slope of central Andes], 2000 m; Philip Hershkovitz (20–27 June 1950). Natural vegetation probably “bosque pluvial Subtropical”.
7. *Quindío*, [Municipio Salento], **El Roble** [4°41'N, 75°36'W; on W slope of central Andes], 7200 ft [2195 m]; Leo E. Miller (9 November 1911). Natural vegetation probably “bosque muy húmedo Montano Bajo”.
8. *Quindío*, [Municipio Salento], **Salento** [4°38'N, 75°34'W; on W slope of central Andes], 7000 ft [2134 m]; Leo E. Miller (November 1911). Natural vegetation probably “bosque muy húmedo Montano Bajo”.
9. *Risaralda*, Municipio Mistrató, Vereda **El Empalado** [ca. 5°22'N, 75°54'W; on E slope of western Andes], 1700–1900 m; Marcela Morales (29 March–3 April 1992). Included sublocalities are “km 13 carretera Mistrató-Pueblo Rico”, “km 13 carretera Mistrató-Costa Rica”, and “km 13 carretera Mistrató-San Antonio del Chamí”. Natural vegetation probably “bosque muy húmedo Montano Bajo”.
10. *Risaralda*, Municipio Mistrató, Vereda **La Jalea**, km 8 carretera Mistrató-San Antonio del Chamí [ca. 5°21'N, 75°53'W; on E slope of western Andes], 1720 m; Marcela Morales (4 April 1992). Natural vegetation probably “bosque muy húmedo Montano Bajo”.
11. *Risaralda*, Municipio Mistrató, Vereda **Mampay**, km 10 carretera Mistrató-San Antonio del Chamí [5°22'N, 75°53'W; on W slope of western Andes], 1950 m; Marcela Morales (7 April 1992). Natural vegetation probably “bosque muy húmedo Montano Bajo”.
12. *Risaralda*, Municipio Pereira, Corregimiento La Florida, Vereda **La Suiza** [ca. 4°44'N, 75°35'W; on W slope of central Andes], 1900–1950 m; Marcela Gómez-Laverde, Angélica Peñuela, and Rocío Polanco (23 February–13 June 1992). Included sublocalities are “al borde de la Quebrada La Hacienda”, “por el camino hacia el Cerro Morro Azul”, and “Quebrada La Hacienda”. Specimens reported from this locality were all collected within the 1992 boundaries of the departmentally-administrated Parque Regional Natural Ucumari, but the sublocalities listed above are now part of the nationally-administrated Santuario de Fauna y Flora del Otún-Quimbaya. See text for a description of local habitats.
13. *Risaralda*, Municipio Pueblo Rico, Vereda **Siató** [5°14'N, 76°02'W; on W slope of western Andes], 1520–1620 m; Marcela Gómez-Laverde (22–23 September 1991). Included sublocalities are “Quebrada la Cristalina”, “Inmediaciones de la Quebrada la Cristalina”, and “borde de la Quebrada la Cristalina”.

- na". See text for a description of local habitats.
14. *Risaralda*, Municipio Santuario, Vereda **El Campamento** [ca. 5°07'N, 75°58'W; on E slope of western Andes], 2500 m; Pedro Sánchez and Marcela Morales (19–23 November 1991). See text for a description of local habitats.
 15. *Risaralda*, Municipio Santuario, Vereda **Los Planes**, Parque Nacional Natural Tatamá [5°08'N, 76°04'W; on E slope of western Andes], 2530 m; Marcela Gómez-Laverde, Pedro Sánchez, and Yaneth Muñoz-Saba (28 October–3 November 1991). See text for a description of local habitats.
 16. *Valle del Cauca*, **Campamento Corea**, three hours on horseback from Cali [not located; in western Andes], 2500–2800 m; P. O. Lowe (17–18 November 1977). Based on elevation, natural vegetation probably "bosque pluvial Montano".
 17. *Valle del Cauca*, Municipio Dagua, **El Queral**, Antena de Tokio [3°29'N, 76°44'W; on W slope of western Andes], ca. 1800 m; Serafín Arango (28 July 1978). Local vegetation probably "bosque pluvial Montano Bajo".
 18. *Valle del Cauca*, Municipio Pichindé, **Finca la Playa** [ca. 3°27'N, 76°37'W; on E slope of western Andes], ca. 1800 m; Lucio Velásquez (26 October–2 November 1966). Local vegetation probably "bosque muy húmedo Montano Bajo". New species of chiggers (Acarina: Trombiculidae) were described by Brennan (1968) from specimens of *Handleyomys fuscatus* collected at this locality.
 19. *Valle del Cauca*, Río Pichindé, **Peñas Blancas** [ca. 3°27'N, 76°43'W; on E slope of western Andes at 2000 m]; Alfred L. Gardner (23–24 October 1974). Local vegetation probably "bosque pluvial Montano Bajo".
 20. *Valle del Cauca*, **San Antonio** [3°30'N, 76°38'W; on E slope of western Andes], 7000–8000 ft [2134–2438 m]; William B. Richardson (5 January–31 March 1911). Local vegetation probably "bosque pluvial Montano Bajo".

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