A New Species of the Rodent Genus *Oecomys* (Cricetidae: Sigmodontinae: Oryzomyini) from Eastern Bolivia, with Emended Definitions of *O. concolor* (Wagner) and *O. mamorae* (Thomas)

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ABSTRACT

We describe a new species of *Oecomys*, *O. sydandersoni* (Cricetidae: Sigmodontinae), from the Parque Nacional Noel Kempf Mercado in eastern Bolivia. One of its diagnostic traits, a derived carotid circulatory plan, provides morphological evidence for its close relationship to *O. concolor* and *O. mamorae* among the 15 species of *Oecomys* currently recognized. Notwithstanding this shared trait, other morphological contrasts and morphometric analyses demonstrate the sharp differentiation of the eastern Bolivian form from both of those species. *Oecomys sydandersoni*, n. sp., is arboreal and was encountered above ground on limbs and woody vines only in densely wooded hummocks scattered through grassland, in contrast to adjacent closed tropical deciduous forest where three other species of *Oecomys* (*O. bicolor*, *O. roberti*, *O. trinitatis*) were obtained. The new species represents the fourth sigmodontine rodent to be named from this restricted region within eastern Bolivia since 1999. Its documentation served as a platform to summarize the nomenclatural history, morphological recognition, and geographic distribution of *O. concolor* (Wagner, 1845) and *O. mamorae* (Thomas, 1906) based on fresh examination of all type material and museum specimens.

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Describimos una nueva especie de Oecomys, O. sydandersoni (Cricetidae: Sigmodontinae), colectado en el Parque Nacional Noel Kempff Mercado al este de Bolivia. Una de las características diagnósticas, el plan de circulación carotideo derivado, provee evidencia de su relación cercana con O. concolor y O. mamorae entre las 15 especies de Oecomys reconocidas hasta la fecha. Además de esta característica compartida, otras características morfológicas y análisis morfológicos demuestran la gran diferenciación de la forma del este boliviano de las otras dos especies. Oecomys sydandersoni, n. sp., es una especie arborícola y fue encontrada sobre el nivel del suelo en ramas y lianas, solamente en montecillos boscosos esparragos por la sabana, a diferencia del bosque adjacente tropical deciduo donde las otras tres especies de Oecomys (O. bicolor, O. roberti, O. trinitatis) fueron encontradas. Esta nueva especie es el cuarto roedor sigmodontino descrito para esta zona del este boliviano desde 1999. Su documentación sirve como una tribuna para compendiar la historia natural, el reconocimiento morfológico, y la distribución geográfica de O. concolor (Wagner, 1845) y O. mamorae (Thomas, 1906) basados en la examinación del material tipo y de especímenes de museo.

INTRODUCTION

Arboreal rodents of the genus Oecomys (Cricetidae: Sigmodontinae) inhabit Neotropical lowland rainforests from southern Central America, throughout the broad reaches of Amazonia, to the Atlantic Forest region of southeastern Brazil (Hall, 1981; Emmons and Feer, 1997; Musser and Carleton, 2005). Described as a subgenus of Oryzomys (Thomas, 1906a), the rank of the taxon thereafter oscillated between subgenus (Goldman, 1918; Ellerman, 1941; Hershkovitz, 1960; Cabrera, 1961; Hall, 1981) and genus (Gyldenstolpe, 1932; Gardner and Patton, 1976; Carleton and Patton, 1976; Carleton and Musser, 1984; Reig, 1984) until broad-scale morphological and molecular studies secured its nomenclatural stature as a monophyletic genus of Oryzomyini (Smith and Patton, 1999; Weksler, 2003, 2006). While phylogenetic appreciation of Oecomys within the oryzomyine kinship web has improved markedly, the number of valid species embraced by the taxon remains uncertain. Hershkovitz (1960) consolidated some 25 species (e.g., Gyldenstolpe, 1932; Ellerman, 1941) into just two, bicolor and concolor, an underestimation of diversity decidedly exposed by site studies in Brazil and French Guiana that have documented four species in sympatry or close parapatry (Carleton et al., 1986, as reported in Voss and Emmons, 1996: appendix 8; Patton et al., 2000; Voss et al., 2001). In a recent taxonomic compendium, Musser and Carleton (2005) acknowledged 15 species of Oecomys but urged the need for continued faunal survey and basic taxonomic revision to enhance understanding of its specific contents.

During inventory of small mammals in eastern Bolivia, conducted over the years 1997–2006, Emmons recovered four species of Oecomys in the Parque Nacional Noel Kempff Mercado (Emmons et al., 2006), Departamento de Santa Cruz. Valid names could be reasonably assigned to three of the four morphologies—O. bicolor, O. roberti, and O. trinitatis—based on current taxonomic understanding, but the identity of the fourth proved to be problematic. Actually, three specimens of this indeterminate form had been earlier collected in adjacent Departamento de Beni and were reported as O. concolor based on certain characteristics of the pelage and cranium (Musser and Carleton, 1993, 2005; Anderson, 1997). Additional study of all material has persuaded us that Emmons’ fourth form represents a new species of Oecomys that we document herein. A key diagnostic feature of the new species involves its derived carotid arterial circulatory pattern, a characteristic shared with two other Oecomys species, O. concolor (Wagner, 1845) and O. mamorae (Thomas, 1906b). Based on this potential synapomorphy (e.g., see Weksler, 2006), we critically differentiate the new species in contrast to O. concolor and O. mamorae and concurrently refine the definitions and distributions of the latter two.
MATERIAL AND METHODS

Specimens examined consisted principally of prepared skins with their associated skulls housed in the following 17 natural history collections, each preceded by the institutional abbreviations adopted throughout the text, tables, and appendices. In addition, type specimens of 44 species-group taxa allocated to *Oecomys* (sensu Musser and Carleton, 2005) have been personally examined by at least one of us, those in North American collections by Carleton and Musser, those in European museums by Musser, and one in Brazil by Emmons. We lacked final catalog numbers for some specimens now deposited in the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), or the Museo de Historia Natural Noel Kempf Mercado, Santa Cruz (MNK), and instead cited the institution’s abbreviation as hyphenated to the collector’s initials and field number. Latitudes and longitudes used for mapping geographic ranges are provided in appendix 1, along with cartographic sources for determining those coordinates. Full provenience as given by the collector and museum catalog numbers are listed in the taxonomic accounts.

AMNH American Museum of Natural History, New York City
ANSP Academy of Natural Sciences, Philadelphia
BMNH The Natural History Museum, London (formerly British Museum of Natural History)
CAS California Academy of Sciences
CM Carnegie Museum of Natural History, Pittsburgh
FMNH Field Museum of Natural History, Chicago
INPA Instituto Nacional de Pesquisas da Amazônia, Manaus
MCZ Museum of Comparative Zoology, Harvard University, Cambridge
MN Museu Nacional da Universidade Federal do Rio de Janeiro
MNK Museo de Historia Natural Noel Kempf Mercado, Santa Cruz
MSB Museum of Southwestern Biology, University of New Mexico, Albuquerque
MSU The Museum, Michigan State University, East Lansing
MVZ Museum of Vertebrate Zoology, University of California, Berkeley
UCONN University of Connecticut, Storrs
UMMZ Museum of Zoology, University of Michigan, Ann Arbor

Five external and 17 cranial dimensions (values in millimeters, mm) were recorded and analyzed to quantify patterns of variation within and between population samples. External variables were generally transcribed from original skin labels as penned by collectors: total length (TOTL); length of tail vertebrae (LT); length of hind foot, including the claw (HFL); length of ear (pinna) from notch (LE); weight in grams (WT). Length of head and body (HBL) was usually calculated by subtracting the length of tail from total length. The external data are presented in tables to convey a general sense of bodily size and proportions but were not enlisted for morphometric evaluations. Crania were viewed under a dissecting microscope when measuring the 15 cranial and two dental variables to 0.1 mm by means of handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations as employed in tables, follow the landmarks defined and illustrated in past oryzomyine studies (Carleton and Musser, 1995; Musser et al., 1998): occipitonasal length (ONE); greatest zygomatic breadth (ZB); breadth of braincase at lateral extremes of lambdoidal ridge (BBC); depth of braincase (DBC); breadth across the exoccipital condyles (BOC); least interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); postpalatal length (PPL); length of bony palate (BPL); length of diastema (LD); length of incisive foramen (LIF); maximum breadth across the incisive foramina (BIF); breadth of the bony palate across the first upper molars (BBP); breadth of the zygomatic plate (BZP);
coronal length of the maxillary toothrow (CLM); width of the first upper molar (WM1).

Relative age was coarsely indexed by degree of molar wear according to the four age-classes (juvenile, young adult, full adult, and old adult) recognized by Carleton and Musser (1989: 4–5). Anatomical terms follow Carleton and Musser (1989), Voss and Carleton (1993), and Musser et al. (1998) for general features of the oryzomyine skull, Bugge (1970) for carotid vessels, Reig (1977) for molar cusps and enamel folds, Wahlert (1985) for cranial foramina, and Voss (1993) for the tegmen tympani; also see Weksler (2006: appendix 2) for a useful synopsis of morphological characters applied in past systematic studies of New World Muroidea.

Univariate and multivariate computations were restricted to specimens assigned to the three adult cohorts (young, full, and old). Standard descriptive parameters (mean, range, standard deviation) were derived for the species samples and are reported in table 4 for the larger samples. One-way analyses of variance, discriminant functions, and principal components were computed using only the craniodental variables, all of which were first transformed to natural logarithms. Principal components (PCs) and canonical variates (CVs) were extracted from the variance-covariance matrix, and their loadings are expressed as Pearson product-moment correlations of the derived components or variates with the original variables. Projections of individual specimen scores onto principal components, or of OTU centroids onto canonical variates, are represented as bivariate scatter plots, usually of the first two factors extracted. Similarity among the predefined geographic samples was graphically summarized using generalized Mahalanobis distances between group (OTU) centroids, and OTUs were amalgamated by the unweighted pair-group method using arithmetic averages. Type specimens were used as cases in multivariate analyses or entered as unknowns for a posteriori OTU classification based on posterior probabilities. All analytical procedures were processed using Systat for Windows (2002, version 10.2).

RESULTS

Within Muroidea, variations in the distal branching of the stapedial artery, a major subdivision of the common carotid, are especially helpful for preliminary taxonomic sorting of specimens, for these arteries leave their imprints on cleaned skulls in the presence/absence of certain cranial foramina and vascular grooves. Morphological surveys of muroid rodents over the past three decades have disclosed three principal themes of stapedial branching that appear to be generally conservative at the taxonomic levels of genus to subfamily (Bugge, 1970; Carleton, 1980; Carleton and Musser, 1984; Voss, 1988; Steppan, 1995). The tribe Oryzomyini is exceptional in that all three circulatory plans are found among its different species groups and genera (Carleton and Musser, 1989; Voss and Carleton, 1993; Musser et al., 1998; Weksler, 2006), and examples of Oecomys exhibit two of these, here simply termed “complete” and “derived.”

A complete carotid circulatory pattern (character state 0 of Carleton, 1980, or pattern one per Voss, 1988) characterizes most recognized species of Oecomys. This pattern, believed to represent the ancestral state for Muroidea (Bugge, 1970; also see Weksler, 2006, for summary of recent studies), retains the supraorbital and infraorbital branches of the stapedial artery (e.g., see Carleton and Musser, 1989: fig. 21B). Osteological landmarks of the supraorbital branch include the squamosal-alisphenoid groove, where it crosses the inner surface of the squamosal and alisphenoid bones, and the sphenofrontal foramen, where it enters the orbit as the opthalmic artery. The infraorbital branch passes over the posterolateral corner of the parapterygoid fossa, typically evidenced by a shallow depression on the pterygoid bone (fig. 1), and reenters the base of the skull through the spacious posterior opening of the alisphenoid canal; it reemerges onto the orbital floor through the anterior alar fissure as the internal maxillary artery. The unreduced orbitomaxillary vessels supplied by the stapedial artery are reflected in the large, distinct stapedial foramen that straddles the petrotympanic fissure (fig. 1). We could verify this
syndrome of cranial traits in the type specimens of 41 species-group taxa assigned to *Oecomys*, representing 13 currently recognized species and their 28 attributed synonyms (table 1).

The derived carotid circulatory plan, characteristic of far fewer members of *Oecomys*, involves loss of both the supraorbital and infraorbital branches of the stapedial artery and attendant cranial modifications (character state 3 of Carleton, 1980, or pattern 3 per Voss, 1988). Lack of a squamosal-alisphenoid groove and sphenofrontal foramen attests the absence of the supraorbital branch; compression or occlusion of the posterior opening to the alisphenoid canal and absence of a posterolateral groove on the parapterygoid plate accompany the loss of the infraorbital branch (fig. 1). With reduction in its distal circulation, the stapedial artery is likewise extremely reduced and the stapedial foramen, if present, is minute (fig. 1). In this condition, supply to the orbitomaxillary region is assumed by a secondary connection between the internal carotid artery and the basally conjoined ophtalmic and
TABLE 1
Character State of the Carotid Circulatory Pattern in Species-group Taxa of Oecomys
(Arranged alphabetically by valid species and chronologically by attributed synonyms.)

<table>
<thead>
<tr>
<th>Species-group Taxa</th>
<th>Type Localities (Holotypes)</th>
<th>Complete(^a)</th>
<th>Derived(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. auyentepui Tate, 1939</td>
<td>Mt. Auyan-tepui, Venezuela (AMNH 131156)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>O. bicolor (Tomes, 1860)</td>
<td>Gualaquiza, Ecuador (BMNH 7.1.1.96)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>dryas Thomas, 1900</td>
<td>Paramba, Ecuador (BMNH 1899.12.5.4)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>benevolens Thomas, 1901</td>
<td>Chimate, Bolivia (BMNH 1.2.1.14)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>rosilla Thomas, 1904</td>
<td>La Union, Venezuela (BMNH 1904.5.7.37)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>nitidulus Thomas, 1910</td>
<td>Essequibo River, Guyana (BMNH 1906.4.8.31)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>florenciae Allen, 1916</td>
<td>Florencia, Colombia AMNH 33863</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>milleri Allen, 1916</td>
<td>Barao de Malgaco, Brazil (AMNH 37117)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>trabecus Allen and Barbour, 1923</td>
<td>Rio Jesusito, Panama (MCZ 19837)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>endersi Goldman, 1933</td>
<td>Barro Colorado Island, Panama (UMMZ 64931)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>phelpsi Tate, 1939(^c)</td>
<td>Mt. Auyan-Tepui, Venezuela (AMNH 131164)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>occidentalis Herskovitz, 1960</td>
<td>Paramba, Ecuador (BMNH 1899.12.5.4)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>O. catherinae Thomas, 1909</td>
<td>Joinville, Brazil (BMNH 9.11.19.24)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>O. cleberi Locks, 1981</td>
<td>Fazenda Água Limpa, Brazil (MN 24131)</td>
<td>+</td>
<td></td>
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</table>

TABLE 1 (Continued)

<table>
<thead>
<tr>
<th>Species-group Taxa</th>
<th>Type Localities (Holotypes)</th>
<th>Complete(^a)</th>
<th>Derived(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. concolor (Wagner, 1845)</td>
<td>Mouth of Rio Cururupi, Brazil (NMW B482)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>marmosurus Thomas, 1899</td>
<td>Maipures, Colombia (BMNH 1899.9.11.38)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>floribunda Thomas, 1894</td>
<td>Mérida, Venezuela (BMNH 1894.9.25.14)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>illectus Bangs, 1898</td>
<td>Pueblo Viejo, Colombia (MCZ 8101)</td>
<td>+</td>
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<tr>
<td>mincae Allen, 1913</td>
<td>Minca, Colombia (AMNH 15332)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>marmorae Thomas, 1906b</td>
<td>Mosetenes, Bolivia (BMNH 1900.8.3.21)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>paricola Thomas, 1904</td>
<td>Igarapê Assu, Brazil (BMNH 1904.7.4.63)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>phaeotis Thomas, 1901</td>
<td>Sagrado, Peru (BMNH 1901.1.1.23)</td>
<td>+</td>
<td></td>
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<tr>
<td>rex Thomas, 1910</td>
<td>Supenaam River, Guyana (BMNH 1910.9.29.17)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>roberti Thomas, 1904</td>
<td>Santa Anna da Chapada, Brazil (BMNH 1903.7.7.67)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>tapajinus Thomas, 1909</td>
<td>Santa Rosa, Brazil (BMNH 1909.3.9.9)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>guianae Thomas, 1910</td>
<td>Supenaam River, Guyana (BMNH 1910.5.4.23)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>rutilus Anthony, 1921</td>
<td>Kartabo, Guyana (AMNH 42910)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>speciosus (Allen and Chapman, 1893)</td>
<td>Princes Town, Trinidad (AMNH 5942/4672)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Species-group Taxa</td>
<td>Type Localities (Holotypes)</td>
<td>Complete&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Derived&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>-------------------</td>
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</tr>
<tr>
<td><em>O. superans</em> Thomas, 1911</td>
<td>Canelos, Ecuador (BMNH 1911.7.19.12)</td>
<td>+</td>
<td></td>
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<tr>
<td><em>palmeri</em> Thomas, 1911</td>
<td>Canelos, Ecuador (BMNH 1911.7.19.13)</td>
<td>+</td>
<td></td>
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<tr>
<td><em>melleus</em> Anthony, 1924</td>
<td>Zamora, Ecuador (AMNH 36560)</td>
<td>+</td>
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<tr>
<td><em>O. trinitatis</em> (Allen and Chapman, 1893)</td>
<td>Princes Town, Trinidad (AMNH 5943/4673)</td>
<td>+</td>
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<tr>
<td><em>subluteus</em> Thomas, 1898</td>
<td>Cundinamarca, Colombia (BMNH 1898.7.3.2)</td>
<td>+</td>
<td></td>
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<tr>
<td><em>fulviventer</em> Allen, 1899</td>
<td>Quebrada Seca, Venezuela (AMNH 14735)</td>
<td>+</td>
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<tr>
<td><em>palmarius</em> Allen, 1899</td>
<td>Quebrada Seca, Venezuela (AMNH 14733)</td>
<td>+</td>
<td></td>
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<tr>
<td><em>tecutus</em> Thomas, 1901</td>
<td>Bugaba, Panama (BMNH 1900.7.11.43)</td>
<td>+</td>
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<tr>
<td><em>klagesi</em> Allen, 1904</td>
<td>El Yagual, Venezuela (AMNH 16966)</td>
<td>+</td>
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<tr>
<td><em>frontalis</em> Goldman, 1912</td>
<td>Corazal, Panama (USNM 171531)</td>
<td>+</td>
<td></td>
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<tr>
<td><em>helvolus</em> Allen, 1913</td>
<td>Villavicencio, Colombia (AMNH 34578)</td>
<td>+</td>
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<tr>
<td><em>vicencianus</em> Allen, 1913</td>
<td>Villavicencio, Colombia (AMNH 34584)</td>
<td>+</td>
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</tr>
</tbody>
</table>

<sup>a</sup>Complete: supraorbital and infraorbital branches of the stapedial artery form major blood supply to the orbitofacial region; sphenofrontal and stapedial foramina present; vascular grooves cross both the inner surface of the squamosal and alisphenoid bones and the posterolateral corner of the parapterygoid fossa; posterior opening to alisphenoid canal large.

<sup>b</sup>Derived: supraorbital and infraorbital branches absent, distal orbitofacial circulation arising from secondary anastomosis to the internal carotid; sphenofrontal foramen absent, stapedial foramen absent or minute; no vascular grooves found on the inner surface of the squamosal and alisphenoid bones or on the posterolateral corner of the parapterygoid fossa; posterior opening to alisphenoid canal irregularly formed or occluded; secondary osseous groove internally crosses the roof of the parapterygoid fossa.

Based on the type as restricted by Musser and Patton (1989).

internal maxillary branches. This anastomosis is suggested by a groove that diagonally crosses the parapterygoid plate, usually observed as a faint line on the translucently thin pterygoid bones, and connects medially with a very short alisphenoid canal (see Carleton and Musser, 1989: fig. 21A); exit from the braincase into the orbital fossa is through the anterior alar fissure. We observed this co-occurrence of osteological features in only three type specimens associated with *Oecomys*, those representing the species *O. concolor* (and its synonym *marmosurus*) and *O. mamorae* (table 1).

All 26 specimens of the unidentified *Oecomys* from eastern Bolivia possess the derived carotid circulatory pattern as just described for *O. concolor* and *O. mamorae*. Nonetheless, they differ appreciably from the latter two species in other aspects of external size, chromatic and textural characteristics of the pelage, and size and shape features of the skull. We underscore the substantial cranial
size and shape differences among the three in
the following multivariate analyses of 17 log-
transformed, craniodental variables as mea-
sured on intact skulls of adult specimens.
Principal component comparisons of the
unidentified *Oecomys* are employed first with
morphologically more similar *O. concolor* and
then with geographically contiguous *O. ma-
morae*, followed by discriminant function
analysis of all three species samples.

Although initially allocated to *O. concolor*,
examples of the eastern Bolivian form prove
to be morphometrically distinct from that
species. The eastern Bolivian form possesses a
generally smaller cranium, as indicated by the
disposition of specimens scores on the first
principal component extracted (fig. 2, top)
and by the uniformly positive and strong
correlation coefficients of most original vari-
ables with PC I (*r* = 0.53–0.96, *P* ≤ 0.001;
table 2). Shape differences are indicated by
significant loadings on the second principal
component, foremost those variables that
reflect size of the incisive foramina (LIF, BIF; table 2). The length and width of the
incisive foramina in the eastern Bolivian form
are larger, both absolutely and relatively, than
the foramina in specimens of *O. concolor*
(table 4). Separation along PC II is also
influenced by the diminutive molars (CLM, WM1) possessed by the eastern Bolivian form
and its relatively short hard palate (BPL)
compared with *O. concolor* (tables 2, 4).
Comparable discrimination and pattern of
variable loadings are apparent in the constel-
lations of scores derived from principal com-
ponent analysis of the eastern Bolivian form
and geographically contiguous populations of
*O. mamorae* (fig. 2, bottom; table 2). Size again
emerges as a latent variable in the dispersion of
scores along PC I (most correlations positive
and large), whereas shape differences involving
fewer select variables appear as important
correlations on PC II. The latter once more
reflect the smaller molar rows observed in the
eastern Bolivian form and its wider incisive
foramina compared with *O. mamorae*; also
noteworthy is the absolutely wider interorbital
region exhibited by the physically smaller
eastern Bolivian form (tables 2, 4).

Given the only marginal contact between
phenotypes apparent in the principal compo-
nent analyses, scatter plots of canonical
variates, extracted from discriminant function
analysis of prior defined groups, predictably
disclose completely nonoverlapping separa-
tion of the eastern Bolivian form from both
*O. concolor*, and *O. mamorae* (fig. 3). Few
variables account for the pronounced hiatus
along CV 1. Notable are the broader inter-
orbit (IOB) characteristic of *O. concolor* and
the sample from eastern Bolivia, as well as
their shorter basicranial axis (PPL), incisive
foramina (LIF), and molar rows (CLM)
compared with those dimensions in *O. ma-
morae* (tables 3, 4). The isolation of the
eastern Bolivian form on CV 2 issues from its
generally smaller size relative to both *O.
concolor* and *O. mamorae* and from many of
the same cranial proportions divulged in the
principal component comparison with *O.
concolor*—spacious incisive foramina (BIF),
shorter bony palate (BPL), and shorter tooth-
row (CLM). Mahalanobis distances between
group centroids summarize these patterns of
variable covariations, revealing that the east-
ern Bolivian form is phenetically closest to
*O. concolor* and that the former two are
approximately equally differentiated from *O.
mamorae*.

**TAXONOMY**

The above morphometric evidence per-
suades us that Emmons’ fourth form from
eastern Bolivia represents a new species,
perhaps closely related to *O. concolor* and *O.
mamorae* as judged from their joint possession
of the derived carotid circulatory pattern. This
species is described next, and the taxonomic
history, morphological recognition, and geo-
graphic distribution of *O. concolor* and *O.
mamorae* are then summarized based on all
specimens personally seen and identified by
us. Synonymies presented below trace earliest
identification and first subsequent usage of
other genus-group and species-group name
combinations.

*Oecomys sydandevsoni*, new species

Figures 4, 5; tables 4, 6

Fig. 2. Projection of specimen scores on first two factors (PC) extracted from principal component analyses comparing samples of *Oecomys*: top, *O. sp. nov. (N = 22)* and *O. concolor (N = 32)*; bottom, *O. sp. nov. (N = 22)* and *O. mamorae (N = 28)*. See table 2 for variable correlations and explanation of percent variance.
TABLE 2
Results of Principal Components Analyses Comparing Adult *Oecomys* sp. novum with *O. concolor* and *O. mamorae*
(Based on 17 log-transformed craniodental variables; see Materials and Methods and fig. 2.)

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>O. sp. novum + O. concolor</em> Correlations</th>
<th><em>O. sp. novum + O. mamorae</em> Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC I</td>
<td>PC II</td>
</tr>
<tr>
<td>ONL</td>
<td>0.96***</td>
<td>0.10</td>
</tr>
<tr>
<td>ZB</td>
<td>0.86***</td>
<td>0.13</td>
</tr>
<tr>
<td>BBC</td>
<td>0.80***</td>
<td>0.02</td>
</tr>
<tr>
<td>DBC</td>
<td>0.53***</td>
<td>0.15</td>
</tr>
<tr>
<td>BOB</td>
<td>0.63***</td>
<td>-0.24</td>
</tr>
<tr>
<td>IOB</td>
<td>0.54***</td>
<td>0.13</td>
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<tr>
<td>LR</td>
<td>0.82***</td>
<td>0.26</td>
</tr>
<tr>
<td>BR</td>
<td>0.84***</td>
<td>-0.04</td>
</tr>
<tr>
<td>BZP</td>
<td>0.76***</td>
<td>0.11</td>
</tr>
<tr>
<td>PPL</td>
<td>0.73***</td>
<td>0.41**</td>
</tr>
<tr>
<td>BPL</td>
<td>0.87***</td>
<td>-0.29*</td>
</tr>
<tr>
<td>LD</td>
<td>0.84***</td>
<td>0.35**</td>
</tr>
<tr>
<td>LIF</td>
<td>0.35**</td>
<td>0.72***</td>
</tr>
<tr>
<td>BIF</td>
<td>-0.18</td>
<td>0.91***</td>
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<tr>
<td>BBP</td>
<td>0.82***</td>
<td>0.11</td>
</tr>
<tr>
<td>CLM</td>
<td>0.72***</td>
<td>-0.40**</td>
</tr>
<tr>
<td>WM1</td>
<td>0.64***</td>
<td>-0.37**</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>0.033</td>
<td>0.011</td>
</tr>
<tr>
<td>% Variance</td>
<td>53.5</td>
<td>17.5</td>
</tr>
</tbody>
</table>

* = P ≤ 0.05; ** = P ≤ 0.01; *** = P ≤ 0.001.

**Holotype:** Museo de Historia Natural Noel Kempff Mercado number 2679, an adult male prepared as round skin and skull; collected 30 July 1997 by Louise H. Emmons (original field number LHE 1415).

External data recorded on the skin tag include: TOTL, 242 mm; TL, 124 mm; HFL, 23 mm; EL, 17 mm; WT, 45 g (see table 4 for craniodental measurements of the type). The animal was noted as having scrotal testes (11 × 7 mm) and was captured “in pampa brush on vines.”

**Type Locality:** Bolivia, Departamento de Santa Cruz, Provincia Velasco, El Refugio Huanchaca, 210 m; 14°46'01"S/61°02'02"W (field coordinates as given by the collector; GPS, map datum WGS84).

On older maps, the locality now known as El Refugio Huanchaca appears only as Huanchaca, a biological station with a few buildings and an airstrip on private property but now partly within the park. The present owners of the estancia renamed it El Refugio, the place name that appears on specimen labels, but in 2004, they appended Huanchaca to their former designation of El Refugio. “El Refugio,” “Huanchaca,” and the combined form “El Refugio Huanchaca,” as applied in eastern Santa Cruz, are one and the same locality.

**Diagnosis:** A species of *Oecomys* (Sigmodontinae: Oryzomyini) characterized by a combination of medium size (HBL ≈ 115–135 mm, HFL ≈ 23–25 mm, ONL ≈ 29–31 mm), relatively short tail (TL ≈ 125–140 mm), absolutely and relatively very wide incisive foramina, smaller molars (CLM ≈ 4.4–4.7), presence of alisphenoid struts, and a derived carotid circulatory pattern (skull lacking squamosal-alisphenoid groove, sphenofrontal foramen, and posterolateral groove on the parapterygoid plate; posterior opening to the alisphenoid canal compressed; stapedial foramen absent; groove dorsally crossing the parapterygoid plate present).

**Referred Specimens:** BOLIVIA: Beni, Río Iténez, ca. 4 km above Costa Marques, 12°29'05"S/64°15'W (AMNH 210023); Río Ité-
CARLETON ET AL.: NEW SPECIES OF *OECEMYS*

**Fig. 3.** Projection of specimen scores on first two canonical variates (CV) extracted from three-group discriminant function analysis of samples representing *Oecomys concolor* (*N* = 32), *O. mamorae* (*N* = 28), and *O. sp. nov.* (*N* = 22). The maximally inclusive polygons enclose specimen scores around an OTU’s centroid; average divergences (Mahalanobis $D^2$) among the three samples are indicated along the lines between the centroids. See table 3 for variable correlations and explanation of percent variance.

**nez, bank opposite Costa Marques, 12°29'S/64°17'W (AMNH 209987); Bahía de los Casara, 20 km W Larangiera, Río Iténez, 13°13’S/62°21’W (AMNH 210012). Santa Cruz, El Refugio, 210 m, 14°46'01"S/61°02'02"W (USNM 588189, 588190; MNK-LHE 1412); 3 km NE El Refugio, Pampa, 14°44'35"S/61°01'20"W (MNK 3763, 3765, 3766, 3772, 3776–3778, 3782, 3788; USNM 584554–584663.

**DISTRIBUTION:** Extreme eastern Bolivia (fig. 6).

**DESCRIPTION:** Size of *O. sydandersoni* medium for the genus (e.g., larger than *O. bicolor* or *O. auyantepui*, smaller than *O. mamorae* or *O. roberti*—see fig. 4 and tables 4, 6 herein; and table 28 in Voss et al. 2001). Fur texture soft and fine; pelage moderately short, hairs about 5–7 mm long over the middle rump. Dorsal pelage ochraceous brown to pale tawny, finely intermixed with black over the middle dorsum and generally bright in tone; more grayish showing on head and flanks. General appearance of ventral pelage a pale to medium gray; hairs of chin, throat, and around inguinal entirely white to base in most specimens; hairs over chest and abdomen gray basally with long white tips. Dorsal-ventral pelage transition moderately defined, without ochraceous lateral line. Eyelids black but no eye-ring per se. Pinnae dark brown to brownish gray, thinly covered with short, ochraceous hairs. Upper surfaces of metatarsals and phalanges covered with whitish to pale ochraceous hairs, general appearance of hind foot a dirty white. Hind-foot conforma-
TABLE 3
Results of Three-group Discriminant Function Analysis of Adult Oecomys sp. novum, O. concolor, and O. mamorae
(Based on 17 log-transformed craniodental variables; see Materials and Methods and fig. 3.)

<table>
<thead>
<tr>
<th>Variable</th>
<th>CV 1</th>
<th>CV 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>ONL</td>
<td>-0.31</td>
<td>0.66***</td>
</tr>
<tr>
<td>ZB</td>
<td>0.08</td>
<td>0.41**</td>
</tr>
<tr>
<td>BBC</td>
<td>-0.23</td>
<td>0.51***</td>
</tr>
<tr>
<td>DBC</td>
<td>0.33</td>
<td>0.24</td>
</tr>
<tr>
<td>BOC</td>
<td>-0.56***</td>
<td>0.50***</td>
</tr>
<tr>
<td>IOB</td>
<td>0.75***</td>
<td>0.12</td>
</tr>
<tr>
<td>LR</td>
<td>-0.28</td>
<td>0.47***</td>
</tr>
<tr>
<td>BR</td>
<td>0.19</td>
<td>0.61***</td>
</tr>
<tr>
<td>BZP</td>
<td>-0.37*</td>
<td>0.35*</td>
</tr>
<tr>
<td>PPL</td>
<td>-0.61***</td>
<td>0.26</td>
</tr>
<tr>
<td>BPL</td>
<td>0.20</td>
<td>0.83***</td>
</tr>
<tr>
<td>LD</td>
<td>0.03</td>
<td>0.41**</td>
</tr>
<tr>
<td>LIF</td>
<td>-0.63***</td>
<td>0.07</td>
</tr>
<tr>
<td>BIF</td>
<td>-0.09</td>
<td>-0.45***</td>
</tr>
<tr>
<td>BBP</td>
<td>0.01</td>
<td>0.52***</td>
</tr>
<tr>
<td>CLM</td>
<td>-0.47***</td>
<td>0.72***</td>
</tr>
<tr>
<td>WM1</td>
<td>-0.09</td>
<td>0.54***</td>
</tr>
<tr>
<td>Canonical correlations</td>
<td>0.93</td>
<td>0.86</td>
</tr>
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<td>Eigenvalue</td>
<td>6.15</td>
<td>2.77</td>
</tr>
<tr>
<td>% Variance</td>
<td>68.9</td>
<td>31.1</td>
</tr>
</tbody>
</table>

*= P ≤ 0.05; ** = P ≤ 0.01; *** = P ≤ 0.001

tion typical of the genus—relatively short and broad; bright white ungual tufts developed on digits II–V; digit V nearly as long as digits II–IV; plantar surface smooth with six large, closely positioned pads, the thenar and hypothenar well developed. Tail slightly longer than head and body; color medium to dark brown all around, slightly paler underneath at the base; caudal hairs short, scarcely visible to the unaided eye and not obscuring fine scale pattern; rudimentary pencil expressed at tip of tail.

Skull ruggedly built for its size, with short rostrum and relatively broad interorbit. Supraorbital shelves present, converging forward such that the least interorbital width is projected relatively anterior between the orbits; free ledge over orbit heavy, approaching an incipient bead; low temporal ridging continues across the lateral parietals in older individuals. Zygomatic arches noticeably expanded at rear and strongly tapered rostrally; dorsal notch of zygomatic plate well defined, plate relatively broad. Posterolateral wall of braincase consistently perforated by small squamosal fenestra, shape slitlike or narrowly ovoid, about one-half the area of the postglenoid foramen; tegmen tympani reduced, touching the ventrolateral squamosal in some specimens but not overlapping it. Alisphenoid struts typically present, delineating a discrete foramen ovale accessorius and masticatory-buccinator foramen. Incisive foramina medium long but very broad, posteriorly terminating just anterior to the anterior root of the M1s; foramina widest toward the rear, posterior ends obtuse (blunt) and anterior ends acute, in some specimens the transition from wide to narrow abrupt. Hard palate basically flat, the palatal gutters shallow and barely evident to the naked eye; palate extends slightly beyond posterior margin of M3s; posterior palatine foramen exits about the middle of M2. Posterolateral-palatal pits well expressed, usually as one large pit with interior perforations plus one or two supernumerary foramina emerging immediately anterior. Mesopterygoid fossa broad and wide, its anterior margin bluntly U-shaped, lacking medial spine or blunt protrusion; roof of mesopterygoid fossa entirely osseous, not perforated by sphenopalatine vacuities. Ectotympanic bulla small, revealing much of the medial periotic, which contributes (as viewed ventrally) to the rear border of the carotid canal.

Upper incisors opisthodont, enamel colored dull yellow-orange to a moderately saturated orange. Molars brachyodont and cuspidate as per the genus, uppers with three roots and lowers with two. M1 with well-formed anterocone and M1–2 with mesoloph. Anterocone broad, anterolinguial and anterolabial conules joined medially, not cleft by anteromedian fold; conules distinct in juveniles and young adults, but definition lost with wear. Mesolophid consistently present on m1–2; ectolophid variably developed, absent in some individuals.

In one-way ANOVAs, none of the 18 craniodental variables demonstrated significant secondary sexual dimorphism (14 ♂, 11 ♀; F = 0.025–3.391; P = 0.975–0.054).

MORPHOLOGICAL COMPARISONS: Specimens of O. sydandersoni can be separated from most
species of *Oecomys* based solely on the osseous character-state differences associated with the complete versus derived carotid arterial patterns (see above descriptions under Results). Other features must be consulted for discrimination from *O. concolor* and *O. mamorae*, the other species so far known to possess a derived carotid pattern. We encountered slight variation in the expression of the derived carotid pattern among the entire series examined of these three species. In some individuals of *O. mamorae* (UMMZ 125456, 133793; UCONN 19187–19189) and *O. sydandersoni* (USNM 584554, 584558), but none of *O. concolor*, a vestige of a squamosal-alisphenoid groove can be detected on the inner wall of the braincase, but no sphenofrontal foramen is present; in these cases, the stapedial foramen persists as a minute pinhole, a tiny aperture in comparison with the full foramen observed in those *Oecomys* with a complete carotid circulatory pattern. Notwithstanding these individual exceptions, a large majority of specimens of *O. mamorae* and *O. sydandersoni* display the typical derived condition as described under Results. Such occasional atavistic reminders of the ancestral character state are to be expected in view of the evolutionary polarity established for carotid arterial patterns in muroid rodents (Bugge, 1970; Carleton, 1980; Voss, 1988; Weksler, 2006).

As currently documented, a wide geographic gap separates the ranges of *O. sydandersoni*, in eastern Bolivia, and *O. concolor*, in southern Venezuela and northwestern Brazil (fig. 6). Examples of *O. sydandersoni* and *O. mamorae*, however, have been collected in close proximity in eastern Bolivia (fig. 6), and their identification may pose greater difficulty. Individuals of *O. sydandersoni* are smaller than those of *O. concolor* and *O. mamorae*, a contrast readily appreciated from variable loadings derived for the first principal component (fig. 2; table 2) or simple inspection of univariate means (table 4). Length of tail is absolutely and relatively shorter in specimens of *O. sydandersoni* (TL = 106% of HBL) compared with those of *O. concolor* (TL = 118% of HBL) and *O. mamorae* (TL = 113% of HBL). The dorsal pelage of *O. sydandersoni* is only slightly longer (5–7 mm), as measured on the rump, than that possessed by the short-furred *O. concolor* (4–5 mm); dorsal pelage of *O. mamorae* is the longest of the three (7–9 mm). *Oecomys sydandersoni* and *O. concolor* resemble one another in dorsal pelage coloration, albeit somewhat darker in tone in *O. concolor*. More grayish hues are evident over the head and flanks of *O. sydandersoni*, compared with a dominant fulvous-brown color in *O. concolor*. The dorsal pelage of *O. mamorae* shows the most gray, ranging from gray to grayish buff, and a buffy to bright ochraceous lateral strip demarcates the upper- and underparts in most specimens. The ventrum of *O. sydandersoni* appears gray, in contrast to dull white, from the chin to inguinin, as observed in most specimens of *O. concolor* and *O. mamorae*; some individuals of the latter two exhibit encroachment of basal gray hairs over the middle abdomen. The dorsal-ventral pelage contrast thus tends to be more sharply marked in *O. concolor* and *O. mamorae*.

Besides cranial size (table 4), subtle but consistent differences in shape provide other reliable means to distinguish the three species (fig. 4). The condition of the supraorbital shelf and interorbital region is similar in *O. sydandersoni* and *O. concolor*, and both differ in the same ways from *O. mamorae*. In the latter species, the interorbit is narrower, and the free edge of the shelf is thinner, less prominent, and confined to the rear of the orbit. Hence, the least interorbital constriction of *O. mamorae* occurs about the middle of orbits (more amphoral), whereas the more prominent shelves in *O. sydandersoni* and *O. concolor* extend farther forward such that the least interorbital width appears more anteriad (more cuneate). The zygomatic plate is broadest in specimens of *O. mamorae* (table 4), and its dorsal notch appears more deeply excised compared with *O. sydandersoni* and *O. concolor*. Posterior termination of the incisive foramina is approximately the same in all three species, reaching the level of the anterior root of the first molars, but their typical shape differs notably among them: anterior and posterior ends acute in *O. concolor*, gently curving along the lateral edges and widest near their middle; foramina also widest at the middle in *O. mamorae*, but outward bowing less pronounced, the foramina appearing more
## Table 4

External and Craniodental Measurements for the Type Series of *O. sydandersoni*, New Species, and Samples of *O. concolor* and *O. mamorae*

(Sample statistics include the mean, ± 1 standard deviation, and the observed range.)

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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTL</td>
<td>242</td>
<td>257.9 ± 16.7</td>
<td>273.2 ± 11.2</td>
<td>296.0 ± 18.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>233–290</td>
<td>255–296</td>
<td>270–230</td>
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<tr>
<td>HBL</td>
<td>118</td>
<td>125.0 ± 12.2</td>
<td>125.4 ± 5.8</td>
<td>139.8 ± 13.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>109–166</td>
<td>115–141</td>
<td>120–170</td>
</tr>
<tr>
<td>TL</td>
<td>124</td>
<td>132.8 ± 8.4</td>
<td>147.9 ± 6.9</td>
<td>158.5 ± 10.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>115–145</td>
<td>137–160</td>
<td>144–180</td>
</tr>
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<td>HFL</td>
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<td>24.1 ± 1.7</td>
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<td>27.3 ± 1.8</td>
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<td>26–29</td>
<td>23–30</td>
</tr>
<tr>
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<td>18.0 ± 1.2</td>
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<td>15–20</td>
<td>17–20</td>
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<tr>
<td>WT</td>
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<td>30–57</td>
<td>41–80</td>
<td>48–120</td>
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<tr>
<td>ONL</td>
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<td>27.7–32.0</td>
<td>30.2–34.3</td>
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<tr>
<td>ZB</td>
<td>16.7</td>
<td>16.5 ± 0.6</td>
<td>17.7 ± 0.6</td>
<td>17.1 ± 0.7</td>
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<td>15.3–17.6</td>
<td>16.6–19.1</td>
<td>15.6–18.1</td>
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<tr>
<td>BBC</td>
<td>11.8</td>
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<td>12.6 ± 0.3</td>
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<td>DBC</td>
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<td>9.3 ± 0.5</td>
</tr>
<tr>
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<td>8.5–9.7</td>
<td>8.8–9.9</td>
<td>7.7–10.0</td>
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<td>BOC</td>
<td>6.6</td>
<td>6.5 ± 0.1</td>
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<td>7.3 ± 0.4</td>
</tr>
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<td>6.3–6.8</td>
<td>6.4–7.3</td>
<td>6.6–7.8</td>
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<tr>
<td>IOB</td>
<td>5.4</td>
<td>5.3 ± 0.3</td>
<td>5.5 ± 0.2</td>
<td>4.9 ± 0.2</td>
</tr>
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<td>5.1–6.0</td>
<td>4.6–5.2</td>
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<td>LR</td>
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<td>7.5–9.1</td>
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<td>8.6–10.0</td>
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<tr>
<td>BR</td>
<td>5.4</td>
<td>5.5 ± 0.3</td>
<td>6.1 ± 0.3</td>
<td>5.8 ± 0.3</td>
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<td>4.7–6.2</td>
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<td>5.4–6.2</td>
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<tr>
<td>PPL</td>
<td>10.4</td>
<td>10.3 ± 0.5</td>
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<td>11.3 ± 0.5</td>
</tr>
<tr>
<td></td>
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<td>9.2–11.4</td>
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<td>10.4–12.0</td>
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<tr>
<td>BPL</td>
<td>5.7</td>
<td>5.6 ± 0.3</td>
<td>6.6 ± 0.3</td>
<td>6.1 ± 0.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.9–6.0</td>
<td>5.9–7.3</td>
<td>5.4–6.9</td>
</tr>
<tr>
<td>LIF</td>
<td>5.6</td>
<td>5.4 ± 0.3</td>
<td>5.3 ± 0.3</td>
<td>5.8 ± 0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.9–5.8</td>
<td>4.5–6.2</td>
<td>5.3–6.3</td>
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<tr>
<td>BIF</td>
<td>2.6</td>
<td>2.6 ± 0.2</td>
<td>2.3 ± 0.2</td>
<td>2.5 ± 0.3</td>
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<td>2.2–2.8</td>
<td>1.8–2.7</td>
<td>2.0–2.9</td>
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<tr>
<td>LD</td>
<td>7.4</td>
<td>7.7 ± 0.5</td>
<td>8.1 ± 0.4</td>
<td>8.0 ± 0.5</td>
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<tr>
<td></td>
<td></td>
<td>6.8–8.7</td>
<td>7.6–9.1</td>
<td>7.2–8.7</td>
</tr>
<tr>
<td>BBP</td>
<td>5.7</td>
<td>5.7 ± 0.2</td>
<td>6.1 ± 0.2</td>
<td>5.9 ± 0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.2–6.2</td>
<td>5.7–6.4</td>
<td>5.4–6.4</td>
</tr>
</tbody>
</table>
nearly parallel sided and narrower; the foramina in O. sydandersoni are noticeably widest toward the rear, the posterior ends obtuse (blunt) and anterior ends acute. The bony palate noticeably projects beyond the posterior margins of the M3s in examples of O. sydandersoni and O. concolor, as in most oryzomyines, but the rear termination of the hard palate in O. mamorae is more or less even with the caudal margin of the M3s. Perhaps in correlation with their longer palates, the posterolateral palatal pits are well developed in the former two—typically as one large pit with interior perforations plus one or two supernumerary foramina emerging immediately anterior—whereas pit construction in O. mamorae is simpler, usually consisting of a single opening. Most of these size and shape contrasts figure prominently in the phenetic patterns derived from the various multivariate analyses and are reflected in the signs and strengths of variable loadings (figs. 2, 3; tables 2, 3; see Results).

The occurrence of the alisphenoid strut, the slim bony column that delineates foramina at the base of the alisphenoid, varies within and among species of oryzomyines (Carleton and Musser, 1989; Voss and Carleton, 1993; Musser et al., 1998), including those of Oecomys (Weksler, 2006). Among the three species with a derived carotid pattern, we observed an alisphenoid strut in most specimens of O. concolor and O. sydandersoni but rarely in those of O. mamorae (table 5). In some individuals, the strut exists as a slender thread (which we counted as present) or is found on only one side of the skull. Used in conjunction with other measurements and qualitative traits, the presence/absence of the alisphenoid strut is useful for identifying specimens of O. mamorae and O. sydandersoni where their ranges approach one another.

Three other species of Oecomys—O. bicolor, O. roberti, and O. trinitatis—have been documented to date in the Parque Nacional Noel Kempff Mercado (Emmons et al., 2006), albeit not in syntopy with O. sydandersoni (see below). The three can be easily differentiated from the new species by a combination of size and qualitative features of the skin and skull. Foremost, they all possess a complete carotid circulatory plan, in contrast to the derived pattern exhibited by specimens of O. sydandersoni. Oecomys bicolor is a diminutive species compared with O. sydandersoni and averages appreciably smaller in every external and cranial dimension quantified (table 6). The dorsal pelage of O. bicolor is shorter and closely cropped, 3–4 mm long at rump (pelage longer in O. sydandersoni, 5–7 mm), and its ventral pelage is uniformly bright white (mostly gray in O. sydandersoni). Furthermore, O. bicolor possesses a relatively shorter tail, only about as long as the head and body (longer, absolutely and relative to the head and body in O. sydandersoni), and the caudal hairs are longer, forming a more distinct terminal pencil (pencil indistinct in O. sydandersoni). Specimens of O. sydandersoni approach those of O. roberti and O. trinitatis in size but average smaller in most dimensions (table 6). Noteworthy are the longer, broader rostra in examples of O. roberti and O. trinitatis (truncate in O. sydandersoni), heavier supraorbital shelf with a distinct bead (incipient bead in O. sydandersoni), and longer bony
Fig. 4. Dorsal (top row) and ventral (bottom row) cranial views (ca. 2 ×) of adult *Oecomys* representing the three species with a derived carotid circulatory pattern: **left pair**, *O. concolor* (USNM 374325, ONL = 31.9 mm), an old adult female from Venezuela, Amazonas, Boca Mavaca, 185 m; **middle pair**, *O. mamorae* (AMNH 260420, ONL = 33.0 mm), an adult female from Bolivia, Santa Cruz, 3.5 km W Estación Pailón, 300 m; **right pair**, *O. sydandersoni* (USNM 584561, ONL = 30.5 mm), new species, an adult female from Bolivia, Santa Cruz, 3 km NE El Refugio.
palate that extends forward beyond the M1s (shorter palate terminates approximately equal with the anterior border of the M1s in *O. sydanderisoni*). The expansive bony palate in these two species inversely correlates with their shorter incisive foramina, which end anterior to the level of the front root of the M1s. Their incisive foramina are also shaped differently, lacking the posterior widening and blunt ends characteristic of *O. sydanderisoni*. The distinctive dorsal pelage of *O. trinitatis*—deep (8–10 mm), palpably luxuriant, and lustrous—at once separates it from examples of *O. sydanderisoni*, as well as those of *O. bicolor* and *O. roberti*. Moreover, the ventrum of *O. trinitatis* is darker gray, the hairs often tipped with buff, its caudal hairs are longer, and, as in *O. bicolor*, the tail possesses a more noticeable terminal pencil compared with *O. sydanderisoni*. The degree of caudal hairiness and pencil development are comparable in *O. sydanderisoni* and *O. roberti*, but the tail of the latter is longer and its dorsal pelage is shorter (3–5 mm in contrast to 5–7 mm in *O. sydanderisoni*).

**ECOLOGICAL NOTES:** At the type locality of El Refugio Huanchaca, Emmons and associates captured 22 of 23 individuals of *O. sydanderisoni* in open savanna characterized by a mosaic of long grasses and smaller clumps of woody vegetation (fig. 7). The grassland is deeply flooded by standing water (ca. 0.5 m) for 1–4 months during the wet season (December–March), and the woody vegetation grows on elevated mounds or hummocks originally formed around termite nests within the grassland. Because cattle no longer graze within the park and the wet grasslands tend to suppress fires, the woody vegetation on these hummocks is dense and well developed, with tall trees in the center and many woody vines. Examples of *O. sydanderisoni* were uniformly collected within the large forested hummocks in snap traps or Sherman live traps placed above ground, up to 2.5 m high on vines, trunks, or branches within arm’s reach. A single individual was captured in closed riverine forest, taken at 1.5 m height on a vine in a shrub along the river’s edge.

Most *O. sydanderisoni* were captured in 1998, when 21 individuals were obtained in the woody hummocks during 1430 trap-nights of collecting effort, along with the forest species *Hylaeamys acritos* (13), *Proechimys longicaudatus* (16), and *Marmosa murina* (1). Four other oryzomyine species (*Cerradomys maracajuensis*, *Holochilus sciureus*, *Oligoryzomys microtis*, *Pseudoryzomys simplex*) and one akodont (*Necromys lenguarum*) were captured in the surrounding grassland matrix. We find it noteworthy that *O. sydanderisoni* was the only arboreal cricetid rodent caught in these woodland islands, that it was the most abundant rodent in that habitat, and that its occurrence was nearly confined to that patchy habitat. Emmons and Bolivian colleagues have tallied over 30,000 trap-nights of survey in nearby habitats, including over 11,000 trap-nights in contiguous semideciduous forests, and captured only a single *O. sydanderisoni*. They have failed to secure the species in dry-ground savanna woodland that lacks dense...
Species of *Oecomys* • *O. concolor* • *O. mamorae* • *O. sydandersoni*, new species. Type localities are indicated by short lines from the four species-group epithets considered herein (*marmosurus*, a junior synonym of *O. concolor*). Gray-shaded areas denote elevations above 1000 meters in the Andean cordilleras and Guianan highlands.

tree clumps (Cerrado proper), or in sporadically flooded “termite” savannas that contain many small shrubs and only small wooded hummocks (<10 m across). Three other species of *Oecomys*—*O. bicolor*, *O. roberti*, and *O. trinitatus*—were obtained in the adjacent, continuous-canopied, semideciduous forests.

These observations portray *O. sydandersoni* as a fairly narrow habitat specialist with a geographically restricted distribution. Such characteristics would perhaps account for its heretofore escape from the eyes of taxonomists and present rarity in collections. As its distribution is so far known, *O. sydandersoni* joins other species with limited geographic ranges that have been recently documented from extreme eastern Bolivia, in the Parque Nacional Noel Kempff Mercado or its vicin-
TABLE 5
Occurrence of Alisphenoid Struts
(−− = struts absent both sides; −+ = strut present on one side; +/+ = struts present both sides.)

<table>
<thead>
<tr>
<th>Species and Country</th>
<th>−−</th>
<th>−+</th>
<th>+/+</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. concolor</td>
<td>1</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Brazil</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Colombia</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Venezuela</td>
<td>1</td>
<td>1</td>
<td>43</td>
</tr>
<tr>
<td>Totals</td>
<td>25</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>O. mamorae</td>
<td>29</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Bolivia</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Brazil</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Paraguay</td>
<td>37</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>43</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>O. sydandersoni</td>
<td>1</td>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td>Bolivia</td>
<td>1</td>
<td>2</td>
<td>23</td>
</tr>
</tbody>
</table>

However, proves to be an example of O. roberti (identified by GGM and reconfirmed by J.L. Patton), a species with a complete carotid circulatory pattern (table 1). Confidence in the sister-group relationship of O. concolor and O. mamorae is thus eroded based on Weksler’s data. Our foremost purpose in documenting the carotid pattern displayed by all Oecomys type specimens (table 1) was to constrain the differential diagnosis of the new species from Bolivia with respect to the most morphologically similar species currently recognized (Musser and Carleton 2005). In addition to possession of the same carotid circulatory plan, the resemblance of O. concolor and O. sydandersoni is striking, as conveyed by the earlier tentative identification of the few known Bolivian specimens as O. concolor (Musser and Carleton, 1993). The fine series later obtained by Emmons allowed morphological and morphometric confirmation of the two as valid species and appreciation of their approximately equivalent level of differentiation from O. mamorae (fig. 3), the third species of Oecomys known to possess the apomorphic carotid condition. Whether the derived carotid arterial pattern constitutes a synapomorphy of these three species or evolved independently will require further molecular and morphological studies based on broader taxon sampling within the genus and among other oryzomyines.

ETYMOLOGY: The first three examples of O. sydandersoni were collected by Sydney Anderson (fig. 8) and members of his field team in 1964 and 1965, along the Rio Iténez in eastern Bolivia. As a fresh-faced assistant curator in 1963, he had revived the earlier natural history explorations in Bolivia undertaken for the American Museum of Natural History, notably those of Anthony and Tate in the 1920s (see chronology of mammalian inventory in Anderson, 1997). Over the next three decades, Syd and his field collaborators amassed impressive series of Bolivian mammals that he utilized in numerous taxonomic reports on this biotically rich but poorly understood country, culminating in his weighty treatise (Anderson, 1997) on the “Mammals of Bolivia, Taxonomy and Distribution.” All the while, he made these collections available to any serious scientist.
### Table 6

External and Craniodental Measurements of the Four Species of *Oecomys* Collected in the Parc Nacional Noel Kempff Mercado, Eastern Bolivia

(Sample statistics include the mean, ± 1 standard deviation, and the observed range.)

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>O. bicolor</em>&lt;sup&gt;a&lt;/sup&gt; (N = 7, 8)</th>
<th><em>O. sydandersoni</em> (N = 21–23)</th>
<th><em>O. roberti</em>&lt;sup&gt;b&lt;/sup&gt; (N = 4, 6)</th>
<th><em>O. trinitatis</em>&lt;sup&gt;c&lt;/sup&gt; (N = 3, 4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTL</td>
<td>211.8 ± 23.4</td>
<td>257.9 ± 16.7</td>
<td>273.5 ± 22.3</td>
<td>260.7 ± 17.6</td>
</tr>
<tr>
<td>HFL</td>
<td>103.9 ± 10.8</td>
<td>132.8 ± 8.4</td>
<td>142.2 ± 13.1</td>
<td>135.3 ± 3.8</td>
</tr>
<tr>
<td>EL</td>
<td>18–21</td>
<td>21–27</td>
<td>24–28</td>
<td>25–27</td>
</tr>
<tr>
<td>WT</td>
<td>29.9 ± 8.1</td>
<td>44.9 ± 7.8</td>
<td>50.5 ± 18.1</td>
<td>45.8 ± 8.7</td>
</tr>
<tr>
<td>ONL</td>
<td>26.8 ± 1.3</td>
<td>29.8 ± 1.2</td>
<td>31.9 ± 1.5</td>
<td>30.7 ± 1.6</td>
</tr>
<tr>
<td>ZB</td>
<td>14.1 ± 0.8</td>
<td>16.5 ± 0.6</td>
<td>16.7 ± 0.9</td>
<td>16.1 ± 0.9</td>
</tr>
<tr>
<td>BBC</td>
<td>11.1 ± 0.4</td>
<td>11.8 ± 0.3</td>
<td>12.1 ± 0.2</td>
<td>11.8 ± 0.4</td>
</tr>
<tr>
<td>DBC</td>
<td>8.4 ± 0.2</td>
<td>9.1 ± 0.3</td>
<td>9.1 ± 0.5</td>
<td>9.0 ± 0.2</td>
</tr>
<tr>
<td>BOC</td>
<td>5.9 ± 0.2</td>
<td>6.5 ± 0.1</td>
<td>6.6 ± 0.1</td>
<td>6.5 ± 0.1</td>
</tr>
<tr>
<td>IOB</td>
<td>4.7 ± 0.2</td>
<td>5.3 ± 0.3</td>
<td>5.5 ± 0.2</td>
<td>5.1 ± 0.3</td>
</tr>
<tr>
<td>LR</td>
<td>7.7 ± 0.6</td>
<td>8.4 ± 0.5</td>
<td>9.7 ± 0.4</td>
<td>9.5 ± 0.6</td>
</tr>
<tr>
<td>BR</td>
<td>4.9 ± 0.3</td>
<td>5.5 ± 0.3</td>
<td>5.9 ± 0.2</td>
<td>5.9 ± 0.5</td>
</tr>
<tr>
<td>PPL</td>
<td>9.4 ± 0.7</td>
<td>10.3 ± 0.5</td>
<td>11.1 ± 1.0</td>
<td>10.4 ± 0.6</td>
</tr>
<tr>
<td>BPL</td>
<td>4.4 ± 0.4</td>
<td>5.6 ± 0.3</td>
<td>6.3 ± 0.2</td>
<td>6.3 ± 0.5</td>
</tr>
<tr>
<td>LIF</td>
<td>4.5 ± 0.3</td>
<td>5.4 ± 0.3</td>
<td>5.2 ± 0.4</td>
<td>5.1 ± 0.3</td>
</tr>
<tr>
<td>BIF</td>
<td>2.1 ± 0.1</td>
<td>2.6 ± 0.2</td>
<td>2.5 ± 0.2</td>
<td>2.3 ± 0.1</td>
</tr>
<tr>
<td>LD</td>
<td>6.7 ± 0.6</td>
<td>7.7 ± 0.5</td>
<td>8.3 ± 0.4</td>
<td>7.6 ± 0.6</td>
</tr>
<tr>
<td>BBP</td>
<td>4.9 ± 0.3</td>
<td>5.7 ± 0.2</td>
<td>5.8 ± 0.2</td>
<td>5.9 ± 0.3</td>
</tr>
<tr>
<td>BZP</td>
<td>2.2 ± 0.3</td>
<td>2.9 ± 0.2</td>
<td>2.8 ± 0.4</td>
<td>3.3 ± 0.3</td>
</tr>
<tr>
<td>CLM</td>
<td>3.75 ± 0.14</td>
<td>4.57 ± 0.14</td>
<td>4.76 ± 0.23</td>
<td>4.80 ± 0.18</td>
</tr>
</tbody>
</table>

<sup>a</sup> Oecomys bicolor

<sup>b</sup> Oecomys roberti

<sup>c</sup> Oecomys trinitatis
TABLE 6
(Continued)

| Variable | O. bicolor<sup>a</sup>  
| (N = 7, 8) | O. sydandersoni  
| (N = 21–23) | O. robert<sup>b</sup>  
| (N = 4, 6) | O. trinitat<sup>c</sup>  
| (N = 3, 4) |
|-----------|------------------|------------------|------------------|------------------|
| WM1       | 1.09 ± 0.04      | 1.32 ± 0.05      | 1.36 ± 0.06      | 1.41 ± 0.08      |
|           | 1.05–1.17        | 1.25–1.40        | 1.28–1.46        | 1.35–1.53        |

<sup>a</sup>Bolivia, Santa Cruz, Parque Nacional Noel Kempff Mercado, 2.5 km NE El Refugio (MNK-LHE 1561; MNK-VCC 13, 20, 132; USNM 584546–584549).

<sup>b</sup>Bolivia, Santa Cruz, Parque Nacional Noel Kempff Mercado, 2.5 km NE El Refugio (MNK-LHE 1658, 1669, 1681, 1685; MNK-VCC 9; USNM 584550, 584551).

<sup>c</sup>Bolivia, Santa Cruz, Parque Nacional Noel Kempff Mercado, Los Fierros (MNK-LHE 1565, 1682; USNM 584552, 584553).

who needed to examine Bolivian specimens and was especially kind in allowing us unrestricted access to oryzomyine rodents, the results of which found their way into our own publications. Such selflessness and sterling ethics are typical of Syd. In the opening paragraph to his 1997 work, Syd wrote, "This work is dedicated to the hypothesis-testers of this world. Everything concluded is subject to further testing” (his laconic drawl, tinged with his gently prodding humor and punctuated by a trailing chortle, permeates this passage in our mind’s ear). New species descriptions form the keystone to all biological hypotheses, and in the spirit of testing one of his conclusions, we are pleased to name this handsome Bolivian endemic of Oecomys in his honor. The species name is thus a patronym in the genitive singular, sydandersoni formed by combining the individual’s familiar name (“Syd”) and surname.

**Oecomys concolor** (Wagner)

*Hesperomys concolor* Wagner, 1845: 147 (type locality: Brazil, Amazonas, Rio Cururiuri, a tributary of the upper Rio Negro, below Sao Gabriel [as amplified by Hershkovitz, 1960: 547]; holotype: NMW B482).

[Oryzomys (Oryzomys) concolor]: Tate, 1932: 3 (name combination, taxonomic history).

**Oryzomys** (**Oecomys**) concolor: Hershkovitz, 1960: 545 (genus-group revision, retention as valid species and nomenclatural subspecies).


**Rhipidomys marmosurus** Thomas, 1899: 378 (type locality: Colombia, Vichada, middle Rio Orinoco, Maipures; holotype: BMNH 1899.9.11.38).

[Oryzomys (Oecomys)] marmosurus: Thomas, 1910: 187 (name combination).

**Oryzomys marmosurus**: Ellerman, 1941: 358 (name combination).

**Oryzomys** (**Oecomys**) concolor concolor: Hershkovitz, 1960: 546 (subgeneric revision, marmosurus allocated as full synonym).

**Oecomys concolor**: Thomas, 1906a: 187 (name combination, marmosurus listed as synonym without indication of rank).

EMENDED DIAGNOSIS: A species of Oecomys (Sigmodontinae: Oryzomyini) characterized by a combination of medium-large size (HFL = 26–28 mm, ONL = 31–33 mm), relatively long tail (TL = 140–155 mm), very short pelage, relatively narrow incisive foramina, presence of alisphenoid struts, and a derived carotid circulatory pattern (skull lacking squamosal-alisphenoid groove, sphenofrontal foramen, and posterolateral groove on the parapterygoid plate; posterior opening to the alisphenoid canal compressed; stapedial foramen absent; groove dorsally crossing the parapterygoid plate present).

**DISTRIBUTION**: Lowland rainforest to the north of the rios Amazonas–Solimões in northeastern Brazil and to the south of the Rio Orinoco in eastern Colombia and southern Venezuela (fig. 6). Known elevational range sea level to 400 m.

**REMARKS**: In 1848, Wagner amplified his initial brief diagnosis (Wagner, 1845) of concolor under Hesperomys, a catchall genus of the middle 1800s whose definition and contents were nearly equivalent to the subfamily Sigmodontinae as its taxonomic boundaries are understood today (translation below by E. Brothers; see appendix 2 for original Latin and German text):
Fig. 7. Characteristic habitat at the type locality of *Oecomys sydandersoni* in the Parque Nacional Noel Kempff Mercado, eastern Bolivia. Individuals of *O. sydandersoni* were captured only in the low-canopied forested patches that grow on elevated hummocks, but not within the surrounding, seasonally flooded grasslands. Photographed by L.H. Emmons in February 2007.

5. *Hesperomys concolor* Wagner. The monochromatic “scharmmaus.”

*Hesperomys concolor* is tawny, abruptly white below, with feet becoming darker, tail naked and as long as the body; with the hairs of the belly a uniform color.

_Hesperomys concolor._ A. Wagner in Archiv für Naturgeschichte 1845: 147.

We have viewed this species initially as a modification of _Hesperomys Anguya_; after I had made a careful comparison with the latter, it appeared more proper to me to consider it a species. It is in all ways very closely related to _H. Anguya_, but the coloring of the dorsum is far livelier, mixed with more red and sprinkled with black. The underside, which is a beautiful white, has hair that is purely of one color, in contrast to the two-colored _H. Anguya_; furthermore, the gray coloring of the cheeks is absent and the feet are covered with brownish hairs; the naked tail, with only short fine hairs, has a dark coloring. The whiskers are black and the ears are haired in the same manner as _H. Anguya_.

<table>
<thead>
<tr>
<th>Body</th>
<th>4° 10&quot;</th>
<th>5° 8&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Ear</td>
<td>6 2/2 [sic]</td>
<td>0 8</td>
</tr>
<tr>
<td>Hindfoot</td>
<td>1 0</td>
<td>1 3</td>
</tr>
</tbody>
</table>

Natterer collected this species at the Curicuriari River in northwestern Brazil.

After Wagner’s description, _concolor_ remained a forgotten name in the early nomenclatural history of oryzomyine rodents until
Tate (1932) associated it with *Oryzomys* (*Oryzomys*). Hershkovitz (1960) correctly recognized *concolor* Wagner as a species of *Oecomys*, ranked as subgenus, but had not examined any type material. Musser’s study of the type specimen of *concolor* (NMW B482; table 7) in 1992 supports Hershkovitz’s genus-group association of the name, the oldest epithet assignable to *Oecomys*. The type is a young adult (sex indeterminate), with only moderate wear on the molars but in full adult pelage. Aspects of the holotype indicate that it was first preserved in alcohol and later stuffed and converted to a museum specimen. The tail is brittle but intact; the pinnae are somewhat tattered and paler than those observed in the recently collected Venezuelan series. The upperparts of the holotype are closely similar in fur length, texture, and color to material from the lowlands of Venezuela except that they are slightly redder, probably a result of initial preservation in alcohol. The chin and throat are gray, and the rest of the underparts are white except along the flanks, where the basal portions of the hairs are pale gray. As emphasized by his designation of the specific name, Wagner was impressed by the all-white underparts of the specimen before him, but coloration of the ventral pelage does vary within the series that we have examined. Many specimens possess small to broad expanses of gray over the middle abdomen, and some exhibit a strong overwash of buffy-tipped hairs; the dorsal-ventral pelage contrast is weakly defined in the latter condition. Impressions of the carotid branching preserved on the skull of the type specimen disclose a derived configuration—no sphen-
frontal foramen or squamosal-alisphenoid groove, minute stapedial foramen, diagonal groove across dorsal surface of parapterygoid bone—the same traits that we have uniformly observed in all other specimens that we identify as *O. concolor*. Further, the type skull bears a strong alisphenoid strut on both sides, a condition observed in nearly all specimens of *O. concolor* examined (table 5).

As mentioned by Wagner, the specimen on which he based his new species was obtained by Johann Natterer (1787–1843), an Austrian naturalist and early collector of birds and mammals in the Amazon Basin. Kurt Bauer of the Naturhistorisches Museum Wien kindly provided additional information about Natterer’s travels and the collecting site of the type (in litt. to GGM, 16 Jan 1984).

I found no information how far up the rio Curicuriari Natterer went, but all indications are, that he stopped just at the mouth or entered the lowest part. *Oe. concolor* seems to be the only mammal collected there, and the itinerary v. Pelzeln [August von Pelzeln, 1825–1891] provided in his work on Natterer’s birds [Pelzeln, 1871] just mentions 5 August 1831 represented by a bird collected there. From his data … and our notes, it is clear that J. Natterer stayed at least until 15th July at the Rio Vaupe/Uaupes and collected at Barcellos/Barcelos about 500 km downriver on the Rio Negro from August 23rd onward.

Thus, the standard coordinates for the mouth of the rio Curicuriari (appendix 1), a southern tributary of the Rio Negro, may reasonably approximate the geographic source of Natterer’s specimen and Wagner’s type of *Hesperomys concolor*.

The holotype of *marmosurus* (BMNH 1899.9.11.38; table 7) possesses a bright ochraceous-tawny dorsum, resembling the more intensely colored specimens in the recent Venezuelan series. The belly is white overwashed with buff. The skull clearly exhibits the key traits of a derived carotid circulatory pattern and possesses well-developed alisphenoid struts on both sides.

The construct of *O. concolor* promulgated by Hershkovitz (1960) consisted of five subspecies (*concolor, speciosus, superans, roberti, bahiensis*) whose collective distribution matched that of the genus in lowland rainforest of Central and South America. The highly variable morphology and pantropical range of his form reflected its composite nature, which embraced, either entirely or in part, at least nine valid species among the synonyms (*auyantepui, catherinae, concolor, flavicans, mamorae, roberti, speciosus, superans, trinitatis*, as per Musser and Carleton, 2005). To our knowledge, only one species-group epithet, *marmosurus* Thomas (1899), properly belongs as a subjective junior synonym of *O. concolor* (Wagner, 1845). Divorced of these other species, *O. concolor* sensu stricto is seen to exhibit a somewhat specialized morphology, with limited boundaries of variation, and this morphology has a very restricted distribution within the genus. The geographic occurrence of *O. concolor* is confined to the Rio Negro West subregion of northern Amazonia, an area of endemism delineated from phylogenetic and distributional studies of neotropical birds (Cracraft and Prum, 1988; Stotz et al., 1996).

**SPECIMENS EXAMINED:** 63, as follows. Brazil—Amazonas, rio Curicuriari, a tributary of the upper Rio Negro, below São Gabriel (NMW B482, holotype of *concolor*); Ilha das Onças, left bank Rio Negro, 01°49’57”S/61°22’49”W (INPA-JLP 16806, 16807, INPA-LC 168, 178, INPA-YL 161); Lago Meduini, left bank Rio Negro, 01°47’07”S/61°23’39”W (INPA-JLP 16795, INPA-LC 176); Macaco, left bank Rio Jau, 24 m, 02°05’01”S/62°02’21”W (INPA-LC 124, 128, 137–139, INPA-YL 127, 129, 131, 133); Macaco, right bank Rio Jau, 02°04’30”S/62°06’21”W (INPA-YL 144, 146, INPA-LC 151, 154); vicinity of Comunidade Tambor, left bank Rio Jau, 02°14’26”S/62°26”W (INPA-MNFS 2038, 2040, 2051, 2057, 2059, 2060); Rio Uaupes, 2 m opposite Tahuapunta, 00°36’N/69°11’W (AMNH 78630); Yavanari, right bank Rio Negro, 00°32’N/64°49’W (AMNH 79400). Roraima, rio Uraicoera (joins the rio Tacutu to form the rio Branco), 03°02’N/60°29’W (BMNH 1933.12.4.5). Colombia—Meta, 18 km S San Juan de Arama, Los Micos, 1300 ft (FMNH 87966, 87968). Vichada, middle rio Orinoco, Mai-pures (BMNH 1899.9.11.38 [holotype of *marmosurus*]). Venezuela—Amazonas, rio Cunucunuma, 48 km NW Esmeralda and 13 km SSW Belén, Acañaña (USNM 406021, 406022); rio Cunucunuma, 56 km NNW Esmeralda, Belén, 150 m (USNM 406013); 68 km SE Esmeralda, Boca Mavaca, 138 m (USNM 406014–406020).
TABLE 7
External and Craniodental Measurements (in mm) of the Type Specimens of *Hesperomys concolor* Wagner, *Rhipidomys marmosurus* Thomas, and *Oryzomys mamorae* Thomas

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>concolor</em></th>
<th><em>marmosurus</em>&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>mamorae</em>&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
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<tbody>
<tr>
<td>HBL</td>
<td>—</td>
<td>124</td>
<td>130</td>
</tr>
<tr>
<td>TL</td>
<td>—</td>
<td>157</td>
<td>168</td>
</tr>
<tr>
<td>HFL</td>
<td>—</td>
<td>26 (28)</td>
<td>27</td>
</tr>
<tr>
<td>EL</td>
<td>—</td>
<td>18</td>
<td>20</td>
</tr>
<tr>
<td>ONL</td>
<td>29.2</td>
<td>33.8</td>
<td>33.1</td>
</tr>
<tr>
<td>ZB</td>
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<td>13.3</td>
<td>12.6</td>
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<td>DBC</td>
<td>—</td>
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<td>9.2</td>
</tr>
<tr>
<td>IOB</td>
<td>5.0</td>
<td>5.8</td>
<td>5.1</td>
</tr>
<tr>
<td>BOC</td>
<td>—</td>
<td>6.9</td>
<td>7.3</td>
</tr>
<tr>
<td>LR</td>
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<td>6.4</td>
</tr>
<tr>
<td>BZP</td>
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<td>3.7</td>
<td>3.4</td>
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<tr>
<td>CLM</td>
<td>4.8</td>
<td>4.9</td>
<td>5.2</td>
</tr>
<tr>
<td>WM1</td>
<td>1.3</td>
<td>1.3</td>
<td>1.5</td>
</tr>
</tbody>
</table>

<sup>a</sup>External data as given by Thomas (1899).

<sup>b</sup>External data as given by Thomas (1906b).

185 m (USNM 374322–374325); Rio Manapiare, San Juan, 155 m (USNM 409862, 409863, 418444); Rio Orinoco, Tamatama, 135 m (USNM 409880, 416712, 416713); Rio Orinoco, Caño Derecho (stream meeting Rio Orinoco on its right bank), 02°48‘N/65°14‘W (AMNH 78069–78072, 78545); Rio Casiquiare, 250 ft, 02°48‘N/65°55‘W (AMNH 77319); 12 mi W Rio Jawasu, left bank of Rio Casiquiare, 01°58‘N, 66°42‘W (AMNH 77328); Rio Casiquiare, El Merly, 03°05‘N/65°55‘W (AMNH 78073, 78074). *Apure*, 60 km NE Puerto Páez, Cinaruco River, Hato Cariben, 76 m (USNM 374321).

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*Oecomys mamorae* (Thomas)

*Oryzomys (Oecomys) mamorae* Thomas, 1906b: 445 (type locality—Bolivia, Cochabamba, Yungas, upper Rio Mamoré, Mosetenes; holotype—BMNH 1900.8.3.21).


*Oryzomys mamorae*: Ellerman, 1941: 358 (name combination).

*Oryzomys mamorae mamorae*: Cabrera, 1961: 405 (retained as species, ranked as nominate subspecies).

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**EMENDED DIAGNOSIS:** A species of *Oecomys* (Sigmodontinae: Oryzomyini) characterized by a combination of medium-large size (HBL = 130–150 mm, HFL = 25–29 mm, ONL = 31–33 mm), relatively long tail (TL = 150–170 mm), narrow interorbit and weakly developed supraorbital ridges, long and narrow incisive foramina, relatively short bony palate and simple posterolateral palatal pits, alisphenoid struts typically absent, and a derived carotid circulatory pattern (skull lacking squamosal-alisphenoid groove, sphenofrontal foramen, and posterolateral groove on the parapterygoid plate; posterior opening to the alisphenoid canal compressed; stapedial foramen absent; groove dorsally crossing the parapterygoid plate present).

**DISTRIBUTION:** Subhumid and gallery forests in savanna and Chaco zones of central...
and eastern Bolivia, contiguous westcentral Brazil, and northern and eastern Paraguay (fig. 6). Known elevational range sea level to 2100 m, most localities within 200–500 m.

Remarks: The cranium of the type specimen of *mamorae* (BMNH 1900.8.3.21), an old adult female, exhibits the essential traits of a derived carotid pattern (no sphenofrontal foramen, stapedial foramen minute), yet it does retain shallow traces of the squamosal-alisphenoid groove on the inner walls of the braincase. As in most specimens of *O. mamorae* that we have examined (table 5), the type lacks alisphenoid struts. Thomas (1906b: 446) critically contrasted his new form *O. mamorae to marmosurus*, here allocated as a junior synonym of *O. concolor*, and captured the consistent proportional differences that we have observed in the larger samples of each species now available: “the distinction of this animal [*O. mamorae*], which may be separated from its only equal in size, *O. (Oe.) marmosurus*, by its narrower interorbital region, less developed orbital ledges, and larger palatal foramina.” The interorbital constriction (IOB) and long incisive foramina (LIF) correlate strongly with the first canonical variate that discriminates specimens of *O. mamorae* from those of *O. concolor* and *O. sydandersoni* (fig. 3; tables 3, 4, 7).

Following Thomas, *O. mamorae* had been retained as a distinctive species by most authors until Hershkovitz (1960) submerged it within his expansive view of *O. concolor*, as a full synonym of *O. c. roberti*. Hershkovitz’s definition of the subspecies confused two distinctive species, *O. roberti* Thomas (1903) and *O. mamorae* Thomas (1906b), which are easily separable from one another and from *O. concolor* (Wagner) proper. Examples of *O. roberti*, like most other *Oecomys*, retain the complete carotid arterial pattern in contrast to the derived condition found in *O. mamorae*. Although the dorsal pelage of both species tends to be pale ochraceous-tawny and the venter mostly white, the cover hairs are typically shorter in *O. roberti* (3–5 mm over the rump) than *O. mamorae* (7–9 mm). In addition, the supraorbital shelf and postero-lateral palatal pits are more pronounced in *O. roberti*. Specimens of *O. roberti* have been recorded in northern and easternmost Bolivia (Anderson, 1997; Emmons et al., 2006), just peripheral to the range of *O. mamorae* (fig. 6), but the two species have yet to be discovered in sympatry.

Specimens of *Oecomys* have been recovered from owl pellets in northeastern Argentina, from the provinces of Chaco (Massoia and Fornes, 1965, as *O. concolor*) and Formosa (Pardiñas and Ramírez-Llorens, 2005, as *O. sp*). By geographic proximity alone, these samples are plausibly referable to *O. mamorae*, but certain measurements reported for the fragmented crania of the Argentine form seem to run larger than *O. mamorae* proper from Bolivia (notably IOB, LIF, BIF, LD, WM1—Pardiñas and Ramírez-Llorens, 2005: table 1). Critical review of variation within nominal *O. mamorae* and comparisons with the Argentine populations are required to verify their specific assignment. Such a review should include those populations documented in eastern Paraguay, to the east of the Paraguay River, reported as *O. concolor* (Myers, 1982) and here referred to *O. mamorae* based on our examinations.

**Specimens Examined:** 128, as follows. **Bolivia**—Bení, Baures (FMNH 117063–117066); Boca del Rio Ibaré (AMNH 211749); Rio Ibaré, 26 km from mouth (AMNH 211718, 211719, 211750–211752); Busurucucú, Yacuma Prov., 200 m (AMNH 263491); Lúcumá, 6 leagues S San Ramón (USNM 460430); Magdalena (FMNH 117055–117058); Rio Bení, El Consuelo, 196 m (NHMS 153); Rio Bení, Puerto Salinas, 226 m (NHMS 62–64, 74–77, 79, 80); Mamoré River (AMNH 211753); Rio Mamoré, Marbán, 240 m (AMNH 129254, 129255); Mamoré, San Joaquín (FMNH 117053, 117059, 117067, 117068; USNM 391302); Rio Tijamuchi, sea level (AMNH 262012); Yutare (FMNH 117060, 117061); Km 35, NW of Yucumá, 253 m (AMNH 264769; MSB 68481); **Chiquisica**, 2 km E Chuhuayacu, 1200 m (MSB 63255); Tomina Province, 40 km from Padilla, Tola Orko, 2100 m (USNM 271581, 271582, 271584–271587); Rio Limón, 1300 m (MSB 63354); Tomina Province, Tihumayu (USNM 290906); Ticuchá, Rio Capirenda (FMNH 72890). **Cochabamba**, Boca Rio Chapare, 825 ft (AMNH 211747); Rio Moli Ichilo (Inst. Roy. Sc. Nat. Belgium 20103, 25297); Todos Santos, 1300 ft (AMNH 38520–38523, 38561, 38563–38566, 38568–38578, 40782–40786; FMNH 21520–21524); Yungas Prov., upper Rio Mamoré, Mission Mosetenes (BMNH 1900.8.3.21 [holotype of *mamorae*], 1900.8.3.24). **La Paz**, 1 mi W Puerto Linares (MSU 33018), **Santa Cruz**, Andrés Ibáñez Prov., Ayacucho (USNM 390655); Cordillera...
Prov., Basilio (USNM 390654); Buena Vista, 350, 450, and 500 m (AMNH 61776; BMNH 26.12.4.52, 28.2.9.42–28.2.9.42, 51.5.23.6; FMNH 25267, 25268, 51907, 51913, 51915); Cordillera Province, 5 km S Choreti, Camiri, 1000 m (CAS 13805; USNM 276602); 3.5 km W Estación Pailón, 300 m (AMNH 260420; MSB 55313); 3 km N and 7 km E Ingeniero Mora, 490–580 m (AMNH 247757); Punta Rieles (AMNH 263101–263104, 263366); San Rafael de Amboro, 400 m (AMNH 262013, 262014, 262119, 262099; MSB 56072); Velasco Prov., Santa Ana (USNM 390656, 391301); 15 km S Santa Cruz, 400 m (MSB 58648); Santa Cruz de la Sierra, 410 m (CM 2146, 2749); Rio Yapacani (FMNH 51914). Brazil—Mato Grosso, Caicara (NMW B475); Descalvados, Uca (FMNH 26643). Mato Grosso do Sul, Fazenda Acurizal (USNM 531278); Rio Paraguai, Uricum de Corumbá (FMNH 26811). Paraguay—Amambay, Bella Vista, Colonia Sargento Duré, 3 km (by road) E Rio Apa (MSB 70699, 70739). Chaco, 50 km WNW Foral Madrejón, Cerro León (UMMZ 125456); 28 km WNW Mayor Pablo La Gorenza, edge Rio La Gorenza (= Rio Timane), San Alfredo (UCONN 19187–19189). Misiones, 40 km S San Ignacio (AMNH 234787). Paragúari, 17 km SW Piribebuy, Saltos de Pirata (UMMZ 133793).

ACKNOWLEDGMENTS

We acknowledge the curators and museum staff who graciously facilitated access to specimens through loans or collections visits over many years, in particular: Kurt Bauer (NMW); Paula Jenkins (BMNH); Sue McLaren (CM); Philip Myers (UMMZ); Bruce Patterson and William T. Stanley (FMNH); James L. Patton (MVZ); and Maria Rutzmoser (MCZ). Eric Brothers (AMNH) kindly translated Wagner’s (1845) original German description of Hesperomys concolor, and Pat Brunauer (AMNH) located and shipped miscellaneous research materials to Musser. The cranial line drawings in figure 1 represent the artistic talent of Patricia J. Wynne, whose keen eye has once again captured the subtle intricacies of the muroid skull in an intelligible manner. We also thank John Steiner (Senior Photographer, NMNH Branch, Smithsonian Photographic Services), who undertook the cranial photography (figs. 4, 5), and Dan Cole (GIS Coordinator, NMNH Office of Information Technology), who supplied the geographic database of South America used for the preparation of the distribution map (fig. 6) and offered guidance in the application of ArcView. Their expert talents and special knowledge were critical to the preparation of this scientific communication. Finally, our communication benefited from the helpful reviews of James L. Patton and Alexandre R. Percequillo. Any errors of omission or commission, of course, remain our own.

Emmons’ field research in Bolivia represents a fruitful collaboration with the Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, and numerous individuals have played vital roles in furthering this research. Damián Rumiz and Kathia Rivero helped with logistics and permits; Alan Weedon and the Weedon Foundation hosted studies at El Refugio Huanchaca; Ian and Barbara Phillips provided logistic support; and Norka Rocha and Veronica Chávez cheerfully provided field assistance. Emmons’ fieldwork was also supported by the Douroucouli Foundation, the National Geographic Society, Wildlife Conservation Society, Amazon Conservation Association, and the W. Alton Jones Foundation. Research in Bolivia was undertaken under permits from the Servicio Nacional de Areas Protegidas and the Dirección General de Biodiversidad y Áreas Protegidas, which kindly facilitated our studies.

REFERENCES


APPENDIX 1

GAZETTEER OF MAPPED LOCALITIES

Cartographic sources included original collector's coordinates as obtained from specimen tags, faunal publications (Anderson, 1997; Handley, 1976), the MCZ ornithological gazetteers on Bolivia, Brazil, Colombia, and Venezuela (Paynter, 1982, 1992, 1997; Paynter and Traylor, 1991), a preliminary gazetteer based on AMNH South American expeditions (AMNH Archives), and the gazetteer from Volume 1 on South American mammals (SAM; Gardner, 2008).

BOLIVIA

Beni, Bahía de los Casara
Beni, Baures
Beni, Boca del Río Ibare
Beni, Busurucucú
Beni, El Consuelo
Beni, Lúcuma
Beni, Magdalena
Beni, Puerto Salinas
Beni, Río Ibare, 26 km from mouth
Beni, Río Iténez, 4 km above Costa Marques
Beni, Río Iténez, bank opposite Costa Marques
Beni, Río Mamoré
Beni, Río Tijamuchi
Beni, San Joaquín
Beni, Yacuma, 35 km N
Beni, Yatxe
Chuquisaca, Chuhuayacu, 2 km E
Chuquisaca, Río Limón
Chuquisaca, Tíchucu
Chuquisaca, Tihumayo
Chuquisaca, Tola Orka
Cochabamba, Mission Mosetenes
Cochabamba, Río Chapare, mouth of
Cochabamba, Río Moile Ichilo
Cochabamba, Todos Santos
La Paz, Puerto Linares
Santa Cruz, El Refugio
Santa Cruz, El Refugio, 3 km NE
Santa Cruz, Ayacucho
Santa Cruz, Basilio
Santa Cruz, Buena Vista
Santa Cruz, Camiri
Santa Cruz, Estación Pailón, 3.5 km W

13°13'S, 62°21'W (Anderson, 1997)
13°35'S, 63°35'W (Anderson, 1997)
14°37'S, 64°57'W (Paynter, 1992)
14°39'S, 66°17'W (Anderson, 1997)
12°29'S, 65°15'W SAM
13°29'S, 64°15'W (Paynter, 1992)
13°20'S, 64°08'W (Anderson, 1997)
14°20'S, 67°33'W (Paynter, 1992)
12°29'S, 64°15'W (Anderson, 1997)
12°29'S, 64°17'W (Anderson, 1997)
12°26'S, 65°11'W SAM
14°56'S, 65°09'W SAM
13°04'S, 64°49'W (Paynter, 1992)
14°52'S, 67°07'W Collector
13°17'S, 64°48'W (Anderson, 1997)
19°43'S, 63°51'W Collector
19°33'S, 64°08'W Collector
20°28'S, 64°04'W (Anderson, 1997)
19°34'S, 64°08'W (Anderson, 1997)
19°27'S, 64°07'W (Anderson, 1997)
16°40'S, 66°03'W (Anderson, 1997)
15°58'S, 64°42'W (Paynter, 1992)
15°57'S, 64°42'W (Paynter, 1992)
16°48'S, 65°08'W (Paynter, 1992)
15°30'S, 67°30'W (Paynter, 1992)
14°46'S, 61°02'W Collector
14°44.58'S, 61°01.33'W Collector
17°51'S, 63°20'W (Anderson, 1997)
18°08'S, 63°19'W (Paynter, 1992)
17°27'S, 63°40'W (Paynter, 1992)
20°06'S, 63°32'W (Paynter, 1992)
17°39'S, 62°45'W Collector
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**BRAZIL**

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<td>Amazonas, Macaco, right bank Río Jaú</td>
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<td>Amazonas, mouth of Río Curicuriari</td>
<td>00°14' S, 66°48' W (Paynter and Traylor, 1991)</td>
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<td>Amazonas, Río Uaupes opposite Tahuapunto</td>
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**COLOMBIA**

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<td>Vichada, Maiiques</td>
<td>05°11' N, 67°51' W (Paynter, 1997)</td>
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**PARAGUAY**

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<tr>
<td>Chaco, Cerro León</td>
<td>20°23' S, 60°19' W SAM</td>
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<td>Chaco, San Alfredo</td>
<td>19°58' S, 60°03' W</td>
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<tr>
<td>Misiones, San Ignacio, 40 km S</td>
<td>26°52' S, 57°45' W (AMNH Archives)</td>
<td></td>
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<tr>
<td>Paraguari, Piribebuy, 17 km SW</td>
<td>25°29' S, 57°03' W</td>
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</tbody>
</table>

**VENEZUELA**

<table>
<thead>
<tr>
<th>Location</th>
<th>Coordinates</th>
<th>Collector</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amazonas, Acacanía</td>
<td>03°32' N, 65°48' W (Handley, 1976)</td>
<td></td>
</tr>
<tr>
<td>Amazonas, Belén</td>
<td>03°39' N, 65°46' W (Handley, 1976)</td>
<td></td>
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<td>Amazonas, Boca del Río Ocamo</td>
<td>02°48' N, 65°14' W (Paynter, 1982)</td>
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<tr>
<td>Amazonas, Boca Mayaca</td>
<td>02°30' N, 65°13' W SAM</td>
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<td>Amazonas, Río Orinoco, Caño Derecho</td>
<td>02°48' N, 65°14' W (AMNH Archives)</td>
<td></td>
</tr>
<tr>
<td>Amazonas, El Merly, Río Casiquiare</td>
<td>03°05' N, 65°55' W (Paynter, 1982)</td>
<td></td>
</tr>
<tr>
<td>Amazonas, Esmeralda</td>
<td>03°10' N, 65°33' W (Paynter, 1982)</td>
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<tr>
<td>Amazonas, Maiiples</td>
<td>05°10' N, 67°47' W (Paynter, 1982)</td>
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<tr>
<td>Amazonas, Río Casiquiare</td>
<td>02°01' N, 67°07' W (Paynter, 1982)</td>
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<tr>
<td>Amazonas, Río Casiquiare, 12 mi W Río Jawasu</td>
<td>01°58' N, 66°42' W (AMNH Archives)</td>
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<td>Amazonas, San Juan de Manapiare</td>
<td>05°05' N, 66°05' W (Paynter, 1982)</td>
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<td>Amazonas, Tama Tama</td>
<td>03°09' N, 65°50' W (Paynter, 1982)</td>
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<td>Apure, Hato Caribén</td>
<td>06°33' N, 67°13' W (Handley, 1976)</td>
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</table>
APPENDIX 2

REDESCRIPTION OF HESPEROMYS CONCOLOR IN THE ORIGINAL GERMAN (WAGNER, 1848: 311–312)


H. fulvus, subtus abrupte albus, pedibus fuscentibus; cauda nuda longitudine corporis; pilis gastraei unicoloribus.

Hesperomys concolor A. Wag. im Arch. F. Naturgesch. 1845. S. 147.

Wir hatten diese Art anfänglich für eine Abänderung von Hesperomys Anguya angesehen; nachdem ich sie aber dahier genauer mit letzterer verglichen habe, scheint es mir doch richtiger sie als eigne Art aufzustellen. Sie ist allerdings mit H. Anguya sehr nahe verwandt, aber die Färbung der Oberseite ist bei ihr weit lebhafter, mit mehr Roth beigemischt, dagegen mit weniger Schwarz gesprenkelt. Die Unterseite, welche schön weiss ist, hat lauter einfärbige Haare, dagegen H. Anguya zweifarbig; ferner fehlt die graue Färbung auf den Wangen des letzteren und die Fusse sind mit bräunlichen Haaren besetzt; der nackte, nur mit kurzen Härchen beflogene Schwanz hat eine dunkle Färbung. Die Schnurren sind schwarz und die Ohren wie bei H. Anguya behaart.

<table>
<thead>
<tr>
<th></th>
<th>H. concolor</th>
<th>H. Anguya</th>
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<tbody>
<tr>
<td>Körper</td>
<td>4&quot; 10&quot;</td>
<td>5&quot; 8&quot;</td>
</tr>
<tr>
<td>Schwanz</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Ohren</td>
<td>0 6 2/2 [sic]</td>
<td>0 8</td>
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<tr>
<td>Hinterfuss</td>
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<td>1 3</td>
</tr>
</tbody>
</table>

Natterer fand diese Art am Flusse Curiecuriar im nordwestlichen Brasilien.

\[\text{This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).}\]