SYSTEMATIC STUDIES OF ORYZOMYINE RODENTS (MURIDAE, SIGMODONTINAE): DIAGNOSES AND DISTRIBUTIONS OF SPECIES FORMERLY ASSIGNED TO *ORYZOMYS* "*CAPITO*"

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 236, 376 pages, 151 figures, 52 tables, 26 appendices
Issued March 16, 1998
Price: $28.00 a copy

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ISSN 0003-0090

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ABSTRACT

We describe the morphological species boundaries and geographic distributions of 10 Neotropical *Oryzomys* based on analyses of museum specimens (skins and skulls, examples preserved in fluid, chromosomal spreads, and information about collection sites from skin tags, field catalogs, and other sources). These species have been regarded as members of an *Oryzomys capito* complex and for a long time were consolidated into a single entity identified as *O. capito*. Our study documents the following:

1. Defining the limits of species within the *O. capito* complex first requires a comprehensive review and rigorous definition of *O. capito* itself. We consider Fischer's (1814) *Mus megacephalus* to be valid and available, designate a neotype to bear the name, and reinstate it as a senior synonym of *capito* Olfers (1818). We then provide a working definition of *O. megacephalus* and its close relative, *O. laticeps*, derived from analyses of morphometric variation, estimates of geographic distributions, and evaluations of synonyms. In our view, *O. megacephalus* occurs in Amazonia but also extends into eastern Paraguay; its synonyms are *capito* Olfers (1818), *cephalotes* Desmarest (1819), *velutinus* Allen and Chapman (1893), *goeldi* Thomas (1897), *modestus* Allen (1899), and *perenensis* Allen (1901).

Oryzomys laticeps Lund (1840) occurs in the Atlantic Forest region of eastern Brazil. We designate a lectotype for *laticeps* and allocate the names *saltator* Winge (1887) and *oniscus* Thomas (1904) as synonyms.

2. We provide the first comprehensive taxonomic revision of *Oryzomys yunganus* Thomas (1902). Its range covers tropical evergreen rainforest formations in the Guiana Region and the Amazon Basin where, as documented by voucher specimens, it has been collected at the same localities as *O. megacephalus, O. nitidus,* and *O. macconnelli.* Specimens of *O. yunganus* can be distinguished from those of the other three by a combination of body size, pelage texture and coloration, pattern of carotid arterial circulation, occlusal patterns of second upper and lower molars, cranial proportions, and chromosomal features. Appreciable intraspecific geographic variation occurs in diploid number of chromosomes and frequency of occurrence of the hypothenar plantar pad, but sampling inadequacies obscure the significance of this variation. Large body size is characteristic of populations in the western Amazon Basin and in the tepui region of eastern Venezuela; smaller size characterizes populations in the Guianas and along the eastern margin of the Amazon Basin. No other scientific name has been correctly associated with the species.

Samples from Mirador, Palmera, and Mera in the western Andean foothills of central Ecuador possess a combination of pelage, cranial, and dental traits that distinguish them from all samples of *O. yunganus*. These specimens are the basis for a new species we describe here, one that is more closely related to *O. yunganus* than to any other member of the former *O.* ''*capito*'' complex.

3. We redescribe *Oryzomys bolivaris* (reviewed by Pine, 1971, under the name *O. bombycinus*), amplify its geographic range, and contrast it with *O. talamancae* and *O. alfaroi,* two sympatric congeners with which it is often confused. A distinctive set of morphological traits allows unambiguous identification of specimens belonging to *O. bolivaris.* It is a trans-Andean species recorded from very wet tropical evergreen rain forests extending from eastern Honduras and Nicaragua through Costa Rica and Panamá to western Colombia and Ecuador. Allen's (1901) *bolivaris* is the oldest name for this species; *castaneus* Allen (1901), *rivularis* Allen (1901), *bombycinus* Goldman (1912), *alleni* Goldman (1915), and *orinus* Pearson (1939) are synonyms.

4. We revise the definition of *Oryzomys talamancae* Allen (1891) provided by Musser and Williams (1985), document additional specimens, describe karyotypes from Ecuadoran and Venezuelan samples, and contrast its morphology, chromosomes, and distribution with those of *O. alfaroi* and *O. megacephalus.* The geographic distribution of *O. talamancae* is also trans-Andean, but it inhabits a wider variety of habitats than does *O. bolivaris.* We also provide a new synonymy and identify the following scientific names as synonyms of *O. talamancae*: *mollipilosus* Allen (1899), *magdalenae* Allen (1899), *villosus* Allen (1899), *sylvaticus* Thomas (1900), *panamensis* Thomas (1901), *medius* Robinson and Lyon (1901), and *carrikeri* Allen (1908).

5. We present hypotheses of species boundaries of four morphologically similar species that we identify as members of the *Oryzomys nitidus* group: *O. nitidus* Thomas (1884), *O. macconnelli* Thomas (1910), *O. russatus* Wagner (1848), and a species described as new. We recognize the four species by morphological and chromosomal traits, and contrast characteristics of each species with one another. One synonym, *boliviae* Thomas (1901), is associated with *O. nitidus,* and two scientific names, *incertus* Allen (1913) and *mureliae* Allen (1915), are allocated to *O. macconnelli.* Synonyms of *O. russatus* are *physodes* Brants (1827), *intermedia* Leche (1886), *coronatus*

Winge (1887), *lamia* Thomas (1901), *legatus* Thomas (1925), *kelloggi* Ávila-Pires (1959), and *moojeni* Ávila-Pires (1959). We designate lectotypes for *russatus* and *intermedia* and identify the holotype of *coronatus.*

Based on voucher specimens, the geographic distribution of *O. nitidus* is mainly along the Andean foothills and adjacent lowlands in Perú, Bolivia, and nearby western Brazil, but scattered records document its eastward extension through south-central Brazil to Paraguay and northeastern Argentina. *Oryzomys macconnelli* inhabits the tropical evergreen rain forests of Amazonia. Its distribution partially overlaps that of *O. nitidus* in western Amazonia, where the two species have been collected together at one locality in Perú, and it is sympatric with the new species, which is recorded only from the lower regions of rios Xingu and Tocantins in northern Pará, Brazil. The distribution of *O. russatus* is documented by specimens from southeastern and south-central Brazil, southern Bolivia, and northern Argentina; its range is allopatric to those of *O. macconnelli,* the new species, and *O. nitidus* except in southern Bolivia, where the latter was collected at the same site with *O. russatus.*

We also examined types and descriptions of taxa associated with *Oryzomys subflavus* and *O. ratticeps* to determine if any of those names actually reference members of the *O. nitidus* group. Although the original description of *subflavus* Wagner (1842) is vague, the holotype clearly represents an example of that very distinctive species; *vulpinus* Lund (1840), for which we designate a lectotype, and *vulpinoides* Schinz (1845) are synonyms of *O. subflavus.*

The oldest name for the species currently known as *Oryzomys ratticeps* is *Mus angouya* Fischer (1814), a name not based on a specimen but on Azara's (1801) description of ‘‘Rat troisième, ou Rat Angouya.’’ Azara's account is so general that it could also apply to individuals of *O. subflavus, O. nitidus,* or *O. russatus.* To stabilize the nomenclature of these species, we designate a neotype for *Mus angouya* Fischer (1814) and treat the following scientific names as synonyms: *buccinatus* Olfers (1818), *leucogaster* Wagner (1845), *ratticeps* Hensel (1872), *rex* Winge (1887), *tropicius* Thomas (1924), and *paraganus* Thomas (1924). We also designate lectotypes for *leucogaster* and *ratticeps.*

We have not analyzed phylogenetic relationships among the species in the former *O.* ‘‘*capito*’’ complex discussed here. Documenting morphological and distributional boundaries of other biological species now grouped in the genus *Oryzomys* (*alfaroi* and its close relatives, for example) must precede, in our view, attempts at phylogenetic reconstruction.

RESUMEN

Describimos los límites morfoespecíficos y las distribuciones geográficas de 10 especies de *Oryzomys* neotropicales, basado en nuestro análisis de ejemplares en museos (pieles y cráneos, cariotipos e información de los sitios de colección obtenida de etiquetas de ejemplares, catálogos del campo y otras fuentes). Estas especies han sido consideradas miembros de un complejo *Oryzomys capito,* y por mucho tiempo fueron unidas como una entidad identificada como *O. capito.* Nuestro estudio documenta lo siguiente:

1. Para definir los límites de especies dentro del complejo *O. capito* se requiere una revisión comprensiva y una definición rigurosa de *O. capito* como tal. Consideramos que *Mus megacephalus* Fisher (1814) es válido y disponible, designamos un neotipo para comprobar el nombre y lo usamos para reemplazar *capito* Olfers (1818). Entonces proveemos una definición práctica de *O. megacephalus* y de su pariente cercano *O. laticeps,* derivada de análisis de variación morfométrica, estimaciones de distribución geográfica y evaluaciones de los nombres sinónimos. A nuestro parecer, *O. megacephalus* se encuentra en la Amazonía con una extensión hasta el interior del este de Paraguay; sus sinónimos son *capito* Olfers (1818), *cephalotes* Desmarest (1819), *velutinus* Allen y Chapman (1893), *goeldi* Thomas (1897), *modestus* Allen (1899) y *perenensis* Allen (1901).

Oryzomys laticeps Lund (1840) se encuentra en la región del bosque atlántico del este de Brasil. Designamos un lectotipo para *laticeps* y asignamos los nombres *saltator* Winge (1887) y *oniscus* Thomas (1904) como sinónimos.

2. Proveemos la primera revisión comprensiva de la taxonomía de *Oryzomys yunganus* Thomas (1902). Su distribución coincide con el bosque húmedo tropical en la región guayana y en el drenaje de la cuenca amazónica donde, como fue documentado por especímenes, ha sido coleccionado en las mismas localidades que *O. megacephalus, O. nitidus* y *O. macconnelli.* Especímenes de *O. yunganus* pueden ser distinguidos de aquellos de los otros tres por una combinación de tamaño de cuerpo, textura y coloración del pelaje, modelo de la circulación arterial carótida, modelos oclusiales de los segundos molares superiores e inferiores, proporciones del cráneo y características de las

cromosomas. Una apreciable variación geográfica intraespecífica se encuentra en el número diploide de cromosomas y en la frecuencia de ocurrencia del tubérculo hipotenar, sin embargo muestras inadecuadas obscurecen la significancia de esta variación. Un tamaño de cuerpo grande caracteriza poblaciones en la cuenca amazónica occidental y en la región tepuyana del este de Venezuela; un tamaño menor caracteriza poblaciones en las Guyanas y en el margen este de la cuenca amazónica. Ningún otro nombre científico ha sido asociado correctamente con esta especie.

Ejemplares de Mirador, Palmera y Mera en la vertiente baja andina del Ecuador central tienen una combinación de características del pelaje, cráneo y dentición que sirve para distinguirlos de todos los ejemplares de *O. yunganus.* Estos especímenes representan la base para una nueva especie que describimos aquí, una especie que tiene una relación más cerca a *O. yunganus* que a cualquier otro miembro del complejo *O.* ‘‘*capito*’’ anterior.

3. Redescribimos *Oryzomys bolivaris* (revisado por Pine, 1971, bajo el nombre *O. bombycinus*), aumentamos su distribución geográfica y la contrastamos con *O. talamancae* y *O. alfaroi,* dos especies congenéricas y simpátricas que frecuentemente son confundidos con ella. Un juego distintivo de características morfológicas permite la identificación positiva de especímenes que pertenecen a *O. bolivaris.* Es una especie trans-andina conocida desde los bosques muy húmedos tropicales en el este de Honduras y Nicaragua, por Costa Rica y Panamá hasta el oeste de Colombia y Ecuador. El nombre *bolivaris* Allen (1901) es el más antiguo para esta especie; *castaneus* Allen (1901), *rivularis* Allen (1901), *bombycinus* Goldman (1912), *alleni* Goldman (1915) y *orinus* Pearson (1939) son sinónimos.

4. Revisamos la definición de *Oryzomys talamancae* Allen (1891) proveída por Musser y Williams (1985), documentamos especímenes adicionales, describimos cariotipos de material ecuatoriano y venezolano, y comparamos y contrastamos su morfología, cariotipos, y distribución con las de *O. alfaroi* y *O. megacephalus.* La distribución geográfica también es trans-andina, pero se encuentra en un variedad más amplia de hábitats que *O. bolivaris.* Además proveemos una sinonomía nueva e identificamos los siguientes nombres científicos como sinónimos de *O. talamancae*: *mollipilosus* Allen (1899), *magdalenae* Allen (1899), *villosus* Allen (1899), *sylvaticus* Thomas (1900), *panamensis* Thomas (1901), *medius* Robinson y Lyon (1901) y *carrikeri* Allen (1908).

5. Presentamos nuestra hipótesis de límites específicos para cuatro especies morfológicamente similares que identificamos como miembros del complejo *Oryzomys nitidus*: *O. nitidus* Thomas (1884), *O. macconnelli* Thomas (1910), *O. russatus* Wagner (1848) y una especie que describimos como nueva. Reconocemos las cuatro especies por características de morfología y cromosomas, y contrastamos las características de estas especies una con la otra. Un sinónimo, *boliviae* Thomas (1901), está asociado con *O. nitidus,* y dos nombres científicos, *incertus* Allen (1913) y *mureliae* Allen (1915) están asignados a *O. macconnelli.* Sinónimos de *O. russatus* son *physodes* Brants (1827), *intermedia* Leche (1886), *coronatus* Winge (1887), *lamia* Thomas (1901), *legatus* Thomas (1925), *kelloggi* Ávila-Pires (1959) y *moojeni* Ávila-Pires (1959). Designamos lectotipos para *russatus* e *intermedia,* e identificamos el holotipo de *coronatus.*

Basado en especímenes comprobantes, la distribución geográfica de *O. nitidus* es principalmente a lo largo de la vertiente baja andina y las contiguas tierras bajas en Perú, Bolivia y el próximo oeste de Brasil; sin embargo, registros dispersos documentan su extensión hacia el este por el surcentral de Brasil hasta Paraguay y el noreste de Argentina. *Oryzomys macconnelli* habita los bosques húmedos tropicales de la Amazonia. Su distribución coincide parcialmente con la de *O. nitidus* en la Amazonia occidental donde ambas especies han sido colectadas juntas en una localidad peruana, y es simpátrica con la especie nueva, la cual se registra solamente en la región del Río Xingu del norte del Pará, Brasil. La distribución de *O. russatus* es documentada por especímenes del sureste y surcentral de Brasil, del sur de Bolivia y del norte de Argentina; su distribución es alopátrica con la de *O. macconnelli,* la de la especie nueva y toda de *O. nitidus* con la excepción de Bolivia austral donde ambas especies fueron colectadas en un solo sitio.

También examinamos los tipos y descripciones de taxa asociados con *Oryzomys subflavus* y *O. ratticeps* para determinar si algunos de estos nombres realmente se refieren a miembros del grupo *O. nitidus.* Aunque la descripción original de *subvus* Wagner (1842) es vaga, el holotipo representa claramente un ejemplar de aquella especie tan distintiva; *vulpinus* Lund (1840), para la cual designamos un lectotipo, y *vulpinoides* Schinz (1845) son sinónimos de *O. subflavus.*

El nombre más antiguo para la especie ahora conocida como *Oryzomys ratticeps* es *Mus angouya* Fischer (1814), un nombre no basado en un espécimen sino en la descripción de Azara (1801) del ‘‘Rat troisième, ou Rat Angouya.’’ El informe de Azara es tan general que podría aplicarse a individuos de *O. subflavus, O. nitidus,* u *O. russatus.* Para estabilizar la nomenclatura de

estas especies, designamos un neotipo para *Mus angouya* Fischer (1814) y tratamos los siguientes nombres científicos como sinónimos: *buccinatus* Olfers (1818), *leucogaster* Wagner (1845), *ratticeps* Hensel (1872), *rex* Winge (1888), *tropicius* Thomas (1924) y *paraganus* Thomas (1924). También designamos lectotipos para *leucogaster* y *ratticeps.*

No hemos analizado relaciones filogenéticas entre las especies en el anterior complejo *O.* ‘‘*capito*’’ discutido aquí. La documentación de límites morfológicos y de distribución de las otras especies biológicas agregadas ahora en el género *Oryzomys* (*alfaroi* y sus parientes cercanos, por ejemplo) debe preceder, a nuestro parecer, intentos de reconstrucción filogenéticas.

RESUMO

Aqui descrevemos os limites morfoespecíficos e a distribuição geográfica de 10 espécies de *Oryzomys* Neotropicais, baseado em análises de exemplares em museus (peles e crânios, espécimes em fluido, cariotipagem de cromossomos, e a informação de sítios de coleta obtida de etiquetas de exemplares, cadernos de campo, e outras fontes). Estas espécies tem sido consideradas membros do complexo *Oryzomys capito* e por um longo período foram consideradas uma única entidade, identificada por *O. capito.* Nosso estudo documenta o seguinte:

1. Definindo os limites de espécies dentro do complexo *O. capito* requer em primeiro lugar uma revisĩao ambrangente, e uma definição rigorosa de *O. capito* como tal. Nós consideramos *Mus megacephalus,* de Fischer (1814), como sendo nome válido e disponível, designamos um neótipo para o nome, e usamos este para substituir *capito* Olfers (1818). Por seguinte providenciamos uma definição prática de *O. megacephalus* e seu parente próximo, *O. laticeps,* derivada de análises de variação morfométrica, estimamos a distribuição geográfica, e avaliamos os sinônimos. Segundo nosso parecer, *O. megacephalus* ocorre na Amazônia mas também se extende ao leste do Paraguai; os sinônimos são *capito* Olfers (1818), *cephalotes* Desmarest (1819), *velutinus* Allen e Chapman (1893), *goeldi* Thomas (1897), *modestus* Allen (1899), e *perenensis* Allen (1901).

Oryzomys laticeps Lund (1840) ocorre na região da Mata Atlântica do leste Brasileiro. Designamos também o lectótipo para *laticeps* e determinamos sinônimos deste os nomes *saltator* Winge (1887) e *oniscus* Thomas (1904).

2. Nós fornecemos a primeira revisão ambrangente taxonômica do complexo *Oryzomys yunganus* Thomas (1902). A distribuição coincide com florestas ombrófilas densas na região das Guianas e bacia amazônica, aonde, tal qual documentado por espécimes em museus, tendo sido coletados nas mesmas localidades que *O. megacephalus, O. nitidus,* e *O. macconnelli.* Espécimes de *O. yunganus* podem ser distinguidos destes três por uma combinação de tamanho corpóreo, textura do pelo e coloração, padrão de circulação arterial da carótide, padrões de oclusão do segundo par de molares superior e inferior, proporções de crânio, e feições de cromossomos. Grande variação geográfica intraespecífica ocorre no número diplóide cromossômico e também na frequência de ocorrência da almofada hipotenar, mas insuficiência na amostragem tornam obscuro o significado desta variação. Grande tamanho corpóreo é característico de populações no leste bacia amazônica e na região de tepuios do leste da Venezuela; tamanho menor caracteriza as populações nas Guianas e ao longo da margem leste da bacia amazônica. Nenhum outro nome tem sido associado corretamente a esta espécie.

Amostras de Mirador, Palmera, e Mera no sopé dos Andes do Equador central possuem uma combinação de pelagem, crânio, e características de dente que distinguem estes de todas as amostras de *O. yunganus.* Estes exemplares são a base para a nova espécie que descrevemos aqui, que é mais aparentada a *O. yunganus* do que qualquer outro membro do complexo *O.* ‘‘*capito*’’.

3. Aqui redescrevemos *Oryzomys bolivaris* (revisto por Pine, 1971, sob o nome de *O. bombycinus*), ampliando sua distribuição geográfica, e contrastando esta espécie com *O. talamancae* e *O. alfaroi,* duas espécies congenéricas simpátricas que com frequência são com ela confundidos. Um grupo de características morfológicas distintas permite uma identificação positiva de exemplares pertencentes a *O. bolivaris.* Esta é uma espécie trans-andina encontrada em florestas ombrófilas densas do leste de Honduras e Nicaragua, Costa Rica e Panamá até o oeste da Colômbia e Equador. O nome *bolivaris* de Allen (1901) é o mais antigo desta espécie; *castaneus* Allen (1901), *rivularis* Allen (1901), *bombycinus* Goldman (1912), *alleni* Goldman (1915), e *orinus* Pearson (1939) são sinônimos.

4. Nós revisamos a definição de *Oryzomys talamancae* Allen (1891) dada em Musser e Williams (1985), documentamos exemplares adicionais, descrevemos cariótipos de amostras do Equador e Venezuela, e finalmente, comparamos e contrastamos sua morfologia, cariótipos e distribuição com aquela de *O. alfaroi* e *O. megacephalus.* A

distribuição geográfica de *O. talamancae* também é trans-andina, mas esta habita uma variedade maior de habitats que *O. bolivaris.* Nós também providênciamos uma nova sinonímia e identificamos os seguintes nomes científicos como sinônimos de *O. talamancae*: *mollipilosus* Allen (1899), *magdalenae* Allen (1899), *villosus* Allen (1899), *sylvaticus* Thomas (1900), *panamensis* Thomas (1901), *medius* Robinson e Lyon (1901, e *carrikeri* Allen (1908).

5. Apresentamos hipóteses de limites específicos de quatro espécies semelhantes que identificamos como membros do grupo *Oryzomys nitidus*: *O. nitidus* Thomas (1884), *O. macconnelli* Thomas (1910), *O. russatus* Wagner (1848), e uma espécie descrita como nova. Nós reconhecemos as quatro espécies por características morfológicas e cromossomicas, e contrastamos as características das espécies uma a uma. Um sinônimo, *boliviae* Thomas (1901), é associado com *O. nitidus,* e dois nomes científicos, *incertus* Allen (1913) e *mureliae* Allen (1915), estes são atribuidos a *O. macconnelli.* Sinônimos de *O. russatus* são *physodes* Brants (1827), *intermedia* Leche (1886), *coronatus* Winge (1887), *lamia* Thomas (1901), *legatus* Thomas (1925), *kelloggi* Ávila-Pires (1959), e *moojeni* Ávila-Pires (1959). Aqui designamos lectótipos para *russatus* e *intermedia,* e um holótipo para *coronatus.*

Baseado em exemplares de museu, a distribução geográfica de *O. nitidus* ocorre principalmente ao longo do sopé das montanhas andinas e planícies adjacentes no Perú, oeste próximo brasileiro, e Bolivia, mas com registros ocasionais documentando uma penetração pelo centro-sul do Brasil até o Paraguai e o nordeste da Argentina. *Oryzomys macconnelli* habita as florestas ombrófilas densas da Amazônia. Sua distribução parcialmente sobrepõem aquela de *O. nitidus* no oeste Amazônico aonde as duas espécies tem sido coletadas juntas numa localidade no Perú, e é simpátrica com a nova espécie, que é registrada somente no Estado de Pará, Brasil. A distribução de *O. russatus* e evidênciada por exemplares do sudeste e centro-sul do Brasil, sul da Bolivia, e norte da Argentina; sua distribuição é alopátrica com aquela de *O. macconnelli,* a nova espécie, e todos *O. nitidus* exceto o sul da Bolivia aonde as duas espécies foram coletados num único sítio.

Também examinamos tipos e descrições de taxa associados a *Oryzomys subflavus* e *O. ratticeps* para determinar se qualquer um destes nomes se referem a membros do grupo *O. nitidus.* Enquanto que a descrição de *subflavus* Wagner (1842) é vaga, o holótipo claramente representa um exemplo de uma espécie bem distinta; *vulpinus* Lund (1840), o qual designamos o lectótipo, e *vulpinoides* Schinz (1845) são sinônimos de *O. subflavus.*

O nome mais antigo da espécie conhecida no momento por *Oryzomys ratticeps* é *Mus angouya* Fischer (1814), a nome que não é baseado num exemplardecriçãosdescriž (1801) ‘‘Rat troisième, ou Rat Angouya.’’ O texto de Azara é tão geral que sua caracterização da espécie também se aplica para indivíduos de *O. subflavus, O. nitidus,* ou *O. russatus.* Para estabilizar a nomenclatura destas espécies, nós selecionamos um neótipo para *Mus angouya* Fischer (1814) e tratamos os seguintes nomes científicos como sinônimos: *buccinatus* Olfers (1818), *leucogaster* Wagner (1845), *ratticeps* Hensel (1872), *rex* Winge (1888), *tropicius* Thomas (1924), e *paraganus* Thomas (1924). Aqui designamos lectótipos para *leucogaster* e *ratticeps.*

Nós não analisamos as relações filogenéticas entre as espécies no antigo complexo *O.* ‘‘*capito*’’ discutido aqui. A documentação de limites morfológicos e de distribuição das outras espécies biológicas no momento agrupadas no gênero *Oryzomys* (*alfaroi* e seus parentes próximos, por exemplo) deve preceder, ao nosso ver, tentativas de reconstrução filogenética.

Questions asked in the museum propelled us between evergreen ramparts along the river until we reached a sandy beach. Leaving bright sky and river murmur, we entered the tall and cool forest. Limbs of great trees and spiraling lianas fractured sunlight into lacy patterns glittering on understory textures; night breezes gave voice to the leaves. Here we hoped to find answers.

–Anon, from the field

INTRODUCTION

Sorting and studying museum specimens, together with their associated data as found in published and unpublished sources, has allowed us to document the morphological and distributional limits 10 ten Neotropical species, most of them formerly assigned to *Oryzomys* ''*capito*.'' These are *O. megacephalus* Fischer (1814), *O. laticeps* Lund (1840), *O. yunganus* Thomas (1902), *O. bolivaris* Allen (1901), *O. talamancae* Allen (1891), *O. nitidus* Thomas (1884), *O. macconnelli* Thomas (1910), *O. russatus* Wagner (1848), and two new species we describe here—one from east-central Ecuador, the other from Brazil. All 10 are distinct elements in lowland rainforest faunas and members of a species complex that share general similarities in body size, pelage traits, cranial form, and dental features. So superficially alike are specimens of this group that, through the years, species have been redescribed several times under different scientific names, collection material has been either incorrectly identified or languished as unidentified in institutions, and ecological and biogeographic accounts based on museum series have proven unreliable. The resulting misapplied and inconsistent usage of names has discouraged production of careful revisionary studies.

Until recently, the many names associated with members of this assemblage were considered to represent a single species, to which first the name *laticeps* (Lund, 1840) and later the name *capito* (Olfers, 1818) were applied. Tate (1939: 189) articulated that view more than 50 years ago:

> The *laticeps* group of *Oryzomys* equals *talamancae* group of Goldman. This is probably the most universally distributed of the tropical groups of *Oryzomys*. In spite of the large number of forms that have received names there exists remarkable uniformity of structure throughout the group. . . . In this division of *Oryzomys* I tentatively group *laticeps, goeldi, yunganus, nitidus, sylvaticus, castaneus, bolivaris, palmirae, gracilis, mollipilosus, villosus, magdalenae, medius, modestus, velutinus, panamensis, talamancae*. It will be seen that the names are greatly concentrated in localities where American and British zoölogists have been most active, namely in the north and northwest of the South American continent. It may be taken as almost axiomatic that mice of this group occur in forests throughout the northern half of South America up to 5000 feet above sea-level.

Tate's opinion, essentially a revision by paragraph unsubstantiated by published data or analyses, has been either forgotten or ignored in the literature.

Twenty-one years later, Hershkovitz (1960) originated the most influential synonymy of *laticeps*/*capito*-like forms in his revision of *Oecomys*, then treated as a subgenus of *Oryzomys*. There he compared the morphology of the arboreal *Oecomys concolor* with *Oryzomys laticeps*, ''a terrestrial species ranging coextensively with *Oecomys*.'' In a brief subscript, Hershkovitz elaborated the contents of *O. laticeps* and asserted the prior availability of *O. capito* (Olfers, 1818; Hershkovitz, 1959, had earlier indicated *capito* to be a senior synonym). His footnote (1960: 544) remains an unfortunate example of taxonomic revision undocumented by specimens or other data and one that misleadingly simplified a complex reality:

> Specific synonyms of *Oryzomys laticeps* include *bolivaris* J. A. Allen, *boliviae* Thomas, *caracolus* Thomas, *castaneus* Thomas, *goeldi* Thomas, *legatus* Thomas, *macconnelli* Thomas, *magdalenae* J. A. Allen, *medius* Robinson and Lyon, *modestus* J. A. Allen, *mollipilosus* J. A. Allen, *oniscus* Thomas, *perenensis* J. A. Allen, *rivularis* J. A. Allen, *saltator* Winge, *sylvaticus* Thomas, *talamancae* J. A. Allen, *velutinus* J. A. Allen, and a few others. *Mus capito* Olfers (1818), based on the ''rat à grosse tête'' of Azara is undoubtedly the same species and antedates *Mus laticeps* Lund (1841). *Mus cephalotes* Desmarest (1819) is another name for Azara's ''rat à grosse tête.''

Except for retention of *macconnelli* as a species, Cabrera (1961) formalized Hershkovitz's arrangement under the name *Oryzomys capito* in his monographic ''Catálogo de los mamíferos de América del Sur.'' Twenty-two names with type localities in South America and three with localities in Panamá and Costa Rica (Hall and Kelson, 1959; Hall, 1981) were associated with *O. capito*; the species was thought to have an extensive geographic distribution in tropical and subtropical lowland forest habitats in northern South America and portions of Central America (fig. 1). Cabrera's classification solidified our misunderstanding of the actual diversity of species contained in the ''*capito*'' complex and obscured appreciation of their distinctive morphologies, ecologies, and phylogenetic relationships.[1]

A turning point in comprehending the systematics of the ''*capito*'' complex emerged in 1976, when Gardner and Patton published their research on ''Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex.'' Although not a formal taxonomic revision, their attention to chromosomal and morphological variation and its significance in unraveling components of the ''*capito*'' complex offered startling counterpoint to Hershkovitz's undocumented lumping. Gardner and Patton not only characterized a species they recognized as *O. capito,* to which they applied some of the synonyms listed in Hershkovitz's footnote, they clearly discerned four related species as well. They amplified the traits that distinguish *O. macconnelli,* thereby corroborating previous identification of the species in checklists (Ellerman, 1941; Cabrera, 1961) and faunal reports (Carvalho and Toccheton, 1969; Husson, 1973; Pine, 1973). They resurrected *O. nitidus,* listed as a subspecies of *O. capito* (Cabrera, 1961) or associated with *O. alfaroi* (Hershkovitz, 1966), and identified diagnostic traits of *O. yunganus,* also buried as a synonym of *O. capito* (Cabrera, 1961). Finally, they suggested that *rivularis,* an Ecuadoran form lumped under *O. capito,* is an earlier name for the species Pine (1971) had reviewed under the name *O. bombycinus.*

Building upon the work of Gardner and Patton (1976) and their own museum researches, other investigators reported on the *O.* ''*capito*'' complex. Musser and Williams (1985) defined *O. talamancae* and summarized distinguishing traits among some species in the *O.* ''*capito*'' complex. Musser and Carleton (1993: 720–725) associated the 21 scientific names relegated to one kind of *Oryzomys* by Hershkovitz (1960) with 12 separate species: *albigularis, alfaroi, bolivaris, capito, intermedius, lamia, legatus, macconnelli, nitidus, oniscus, talamancae,* and *yunganus.* They admitted that the status of *lamia* and *legatus* was provisional with regard to *O. intermedius* and *O. nitidus* and needed further study.

We define 10 species of *Oryzomys* herein, but to delimit their morphological and geographic boundaries required that we construct a working definition of *O.* ''*capito*''. Even divorced of the several species long confused under it—*O. bolivaris, O. russatus* (formerly known as *intermedius*), *O. macconnelli, O. nitidus, O. talamancae,* and *O. yunganus*—the range of morphological variation, number of valid species, and attendant nomenclatural issues involving the residuum of ''*capito*'' are entangled and complex. Accordingly, our review has relied on direct examination and analyses of specimens of so-called ''*capito*'' from throughout its range. These morphometric results, supplemented with chromosomal data and other evidence, are considered with respect to the delineation of species and in light of the scientific names that may apply. In doing so, we defend the use of *O. megacephalus* (Fischer, 1814) and *O. laticeps* (Lund, 1840) as older synonyms for the species currently known respectively as *O. capito* (Olfers, 1818) and *O. oniscus* (Thomas, 1904). We also highlight the potential significance of the taxon *perenensis* Allen (1901) in future studies designed to unambiguously diagnose *O. megacephalus.*

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[1] The names *palmirae* and *gracilis* were included by Tate (1939), and *caracolus* by Hershkovitz (1960), in their respective versions of the *capito*/*laticeps* group. Both *palmirae* and *gracilis* were subsequently associated with *O. alfaroi* by Cabrera (1961: 383), and *caracolus* with *O. albigularis* by Hershkovitz (1966: 137). We have studied the holotypes upon which these names are based, concur with those allocations, and do not regard them as representing species in the *O.* ''*capito*'' complex.

Fig. 1. Geographic distribution of type localities for most of the scientific names informally associated with the *Oryzomys* "*laticeps*" group by Tate (1939) and *Oryzomys* "*capito*" complex by Hershkovitz (1960). Except for *macconnelli*, Cabrera (1961), in his influential catalog of South American mammals, explicitly subsumed all these names tied to South American types under a single species, *O. capito*. Names based on types collected in Panamá and eastern Costa Rica were also listed as synonyms of *O. capito* in the first (Hall and Kelson, 1959) and second (Hall, 1981) editions of the *Mammals of North America*. Stippling approximates composite geographic ranges of the species to which these names apply.

Here and elsewhere, we emphasize that our overview of ''*capito*'' does not constitute a critical taxonomic revision; it does, however, supply a more than sufficient basis for differential diagnoses and comparisons of the eight related species that form the nucleus of our report.

Next, we detail the morphological and geographic boundaries of those eight species, and present their treatment under three logically contained subheadings: the *Oryzomys yunganus* group—*O. yunganus* and a new species from Ecuador, both indigenous to Amazonia; the trans-Andean species, *Oryzomys bolivaris* and *O. talamancae*; and the *Oryzomys nitidus* group—*O. nitidus, O. macconnelli,* a new species from Brazil, and *O. russatus.* In each section or species account, we provide gazetteers of original collection localities; allocate specimens (by their museum catalog or collector's field numbers) to species; summarize geographic distributions, records of sympatry, and ecological occurrences; introduce the nomenclatural history and taxonomic literature pertinent to understanding our usage of a specific epithet; distill and illustrate key diagnostic features for each species and contrast them with one another and with morphologically similar, sympatric congeners; and assess intraspecific patterns of geographic variation by using cranial and dental variables and provide tabular and illustrative summaries of that variation.

A section on taxonomy and related information follows. There we summarize the scientific names and attendant data that we associate with each of the species recognized (including *O. megacephalus* and *O. laticeps,* the only members of the *O.* ''*capito*'' group as we redefine it here), explain the reasons for these allocations, and clarify locations of some type localities. We also describe the basis for each of the scientific names associated with *O. subflavus* and the species currently known as *O. ratticeps* within the context of determining whether any of them actually apply to members of the former *O.* ''*capito*'' complex.

We conclude with an overview on the former *Oryzomys* ''*capito*'' complex, our version of its contents, and highlight morphological traits that distinguish the species extracted from that complex.

Identifying specimens in museum collections (the primary source of data accessible to us) and identifying limits of each specific entity provide an empirical framework of morphologically defined species and geographic occurrence. These activities are important in selfish and altruistic contexts. Personally, we satisfy our curiosity about the number of species, along with their characteristics, that are integral parts of particular Neotropical ecosystems. Simultaneously, we reinforce our confidence to consistently recognize these faunal components, which enlarges our understanding of the profound complexity of tropical evergreen rain forests in Central and South America. Publicly, our results contribute to other kinds of inquiries about these forests and contiguous biomes. For example, estimates of mammalian biodiversity and delineation of biogeographic patterns can only follow credible definitions of species and objective criteria by which to identify them, either firsthand by collection and study of museum specimens or secondarily from published descriptions and lucid interspecific comparisons.

Reliable characterization of species is an essential step toward eventual reconstruction of phylogenetic alliances among them as well as illumination of zoogeographic patterns from refinement of their geographic distributions. Neotropical species now included in *Oryzomys* and other oryzomyine genera are, in general, poorly defined; variation in morphological and other kinds of character data within each and the boundaries of geographic ranges are unknown. Data provided here, along with results from published taxonomic revisions and those still in preparation, ultimately relate to broader inquiries into the diagnosis of the genus *Oryzomys* itself and to reconstruction of oryzomyine phylogeny (Myers and Carleton, 1981; Musser and Williams, 1985; Carleton and Musser, 1989, 1995; Musser and Patton, 1989; Musser and Carleton, 1993, unpubl. ms; Voss, 1991; Voss and Myers, 1991; Voss and Carleton, 1993).

MATERIALS AND METHODS

SPECIMENS AND ABBREVIATIONS: The specimens we examined are identified throughout the main body of the text, the tables, and appendices by the institutional or collectors' initials defined below, in combination with catalog or field numbers.

AMNH	American Museum of Natural History, New York City
ANSP	Academy of Natural Sciences, Philadelphia
ARG	Initials accompanying field numbers of uncataloged specimens from Argentina in Oklahoma Museum of Natural History, Norman
BMNH	British Museum (Natural History), London [now Natural History Museum, London]
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago [now Field Museum, Chicago]
JLP	Field numbers of James L. Patton, Museum of Vertebrate Zoology, University of California, Berkeley (These numbers, along with those bearing the initials MNFS and JUR, apply to specimens collected along the Rio Juruá in western Brazil and will eventually be cataloged in the Museum of Vertebrate Zoology, the Instituto Nacional de Pesquisas da Amazônia at Manaus, or the Museu Parâense Emilio Goeldi in Belém; Patton, personal commun.; letter in archives of AMNH, Mammalogy)
JUR	Field numbers of Jay R. Malcolm, Centre for Biological Conservation, University of Florida, Gainesville (see note under JLP)
KU	Museum of Natural History, University of Kansas, Lawrence
LACM	Los Angeles County Natural History Museum, Los Angeles
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MHNLS	Museo de Historia Natural La Salle, Caracas
MN	Museu Nacional, Rio de Janeiro
MNFS	Maria Nazareth F. da Silva, Museum of Vertebrate Zoology, University of California, Berkeley, and Departamento de Ecología, Instituto Nacional de Pesquisas da Amazônia, Manaus (see note under JLP)
MNHN	Museum National d'Histoire Naturelle, Paris
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
MZUSP	Museu de Zoología, Universidade de São Paulo, São Paulo
NMW	Naturhistorisches Museum Wien, Wien
NW	Field numbers of Neal Woodman, Museum of Natural History, University of Kansas, Lawrence
OMNH	Oklahoma Museum of Natural History, Norman
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden [now Nationaal Natuurhistorisch Museum, Leiden]
RMT	Field numbers of Robert M. Timm, Museum of Natural History, University of Kansas, Lawrence
ROM	Royal Ontario Museum, Toronto
TTU	The Museum, Texas Tech University, Lubbock
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UZM	Universitets Zoologisk Museum, Copenhagen
ZMB	Zoologisches Museum und Institut für Spezielle Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin
ZSM	Zoologische Staatssammlung München, München

Most of the materials we examined consisted of conventional museum study skins with accompanying skulls. We studied only the skulls in a few large samples from Perú and along the Rio Juruá in western Brazil.

Gazetteers: Localities from which samples were collected, along with either the institutional initials and catalog number or collectors' initials and field number of each specimen examined, are listed in a gazetteer placed in the text of each species or species-group account. Descriptions of locality and elevation (recorded in meters or feet, depending on the convention used by the collector) were taken from labels attached to skins. These basic data were enhanced where necessary by relevant information from field journals, other archival material, and published expeditionary accounts and gazetteers; sources are cited in the locality entry.

Measurements: These were obtained from

skins, skulls, and dentitions and are expressed in millimeters (mm); weight (in grams) was also recorded. External measurements, in the order that they appear in tables, are defined below:

LHB	length of head and body (= total length minus tail length)
LT	length of tail
TSR/CM	number of scale rows per centimeter of tail
LHF	length of hind foot, including claw
LE	length of ear
LDF	length of dorsal fur (excluding guard hairs)
LMV	length of longest mystacial vibrissae
LSV	length of longest superciliary (supraorbital) vibrissae
LGV	Length of longest genal vibrissae

Measurements of total, tail, hind foot, and ear lengths that we recorded are generally those made by collectors recorded on skin labels. We measured the dry hind foot of each holotype to obtain a uniform value of more utility for comparisons than those noted on the skin label. Measurements of body and appendages made by different collectors vary (because some measured more accurately than others, and not all collectors used the same endpoints), especially length of ear. We relied on these data for a general sense of size but were careful about evaluating the significance of any differences in certain external measurements among samples within a species and between samples of species.

Other data from skins were taken by us. We counted scale rows on the tail (along a centimeter section about one-third of the way from the body) and measured pelage thickness on dry stuffed skins. The latter was estimated by inserting the end of a short ruler through the dorsal coat to the skin, forcing the fur back so it was erect along the base of the ruler, and estimating average length of overhairs (that is, excluding guard hairs). Lengths of vibrissae were taken from dry skins and a few specimens preserved in fluid. Vibrissal terminology is that defined by Brown (1971).

Weights are from skin labels or field catalogs.

Dial calipers (graduated to 0.01 mm) were used to obtain measurements of the following cranial and dental dimensions (listed in the sequence that they appear in the tables):

ONL	occipitonasal length
ZB	greatest zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
LB	lambdoidal breadth
HBC	height of braincase (ventral limit, which is unclear in fig. 2, is surface of basioccipital)
BZP	breadth of zygomatic plate
LD	length of diastema
LBP	length of bony palate
BBP	breadth of bony palate across first upper molars
PPL	postpalatal length
LIF	length of incisive foramina
BIF	breadth of incisive foramina
CLM1–3	crown length of maxillary toothrow
BM1	breadth of first upper molar

Limits of these measurements are shown in figure 2; most are the same as defined by Musser (1979), except that the breadth of the bony palate is the distance between labial edges of the first upper molars, and lambdoidal breadth is a measure of braincase width between lambdoidal ridges. All specimens used in the numerical analyses were measured by G. G. Musser.

SEXUAL DIMORPHISM: Variation in morphological traits that might be related to sex is not addressed by us. Females and males were combined in all analyses. As we sorted specimens, we did not detect any noticeable size variation between sexes of comparable ages, an observation also recorded by Goldman (1918) in his monograph on North American *Oryzomys*; morphometric studies of oryzomyines have found only slight or insignificant sexual variation in variables measured (Musser and Williams, 1985; Carleton and Musser, 1989; Voss, 1991; Carleton and Musser, 1995).

AGE CRITERIA: We sorted specimens of *Oryzomys bolivaris* and *O. talamancae* collected at the same locality in Panamá into ‘‘adults,’’ ‘‘young adults,’’ ‘‘young adult-juveniles,’’ and ‘‘juveniles’’; those categories are defined where we contrast the two species in the account of *O. bolivaris.* Otherwise, our analyses of variation in samples of all the other species discussed here rely on

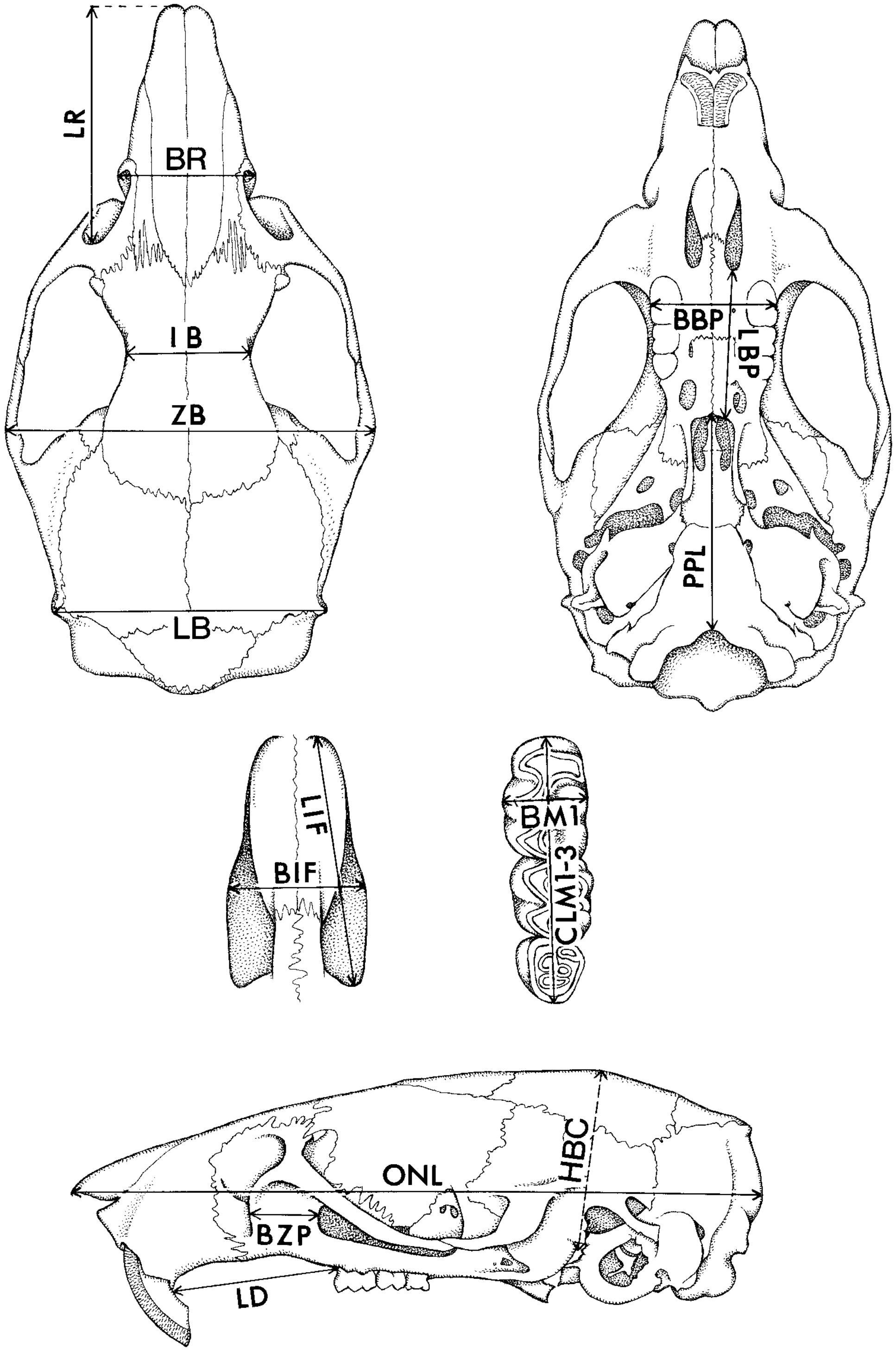

Fig. 2. Views of the cranium (dorsal, ventral, lateral), right maxillary molar row, and incisive foramina of an adult *Oryzomys alfaroi* illustrating limits of the 14 cranial and 2 dental measurements recorded for specimens of *Oryzomys* we measured. Abbreviations are defined in text.

''adult'' material, which combines the growth stages from young to old adults. To be classified as adult, a specimen had to be covered by full adult pelage—not the gray or blackish juvenile coat or the transitional molt from juvenile to adult fur—and have completely erupted third molars. Sorting age variation into additional categories would have reduced most samples to a point where quantitative results would be less reliable.

ANATOMY: Terminology we use follows Brown (1971) for external features of the head, Reig (1977) for the dentition, Bugge (1970) for the cephalic arteries, Wahlert (1985) for the cranial foramina, and Carleton (1980) and Carleton and Musser (1989) for cranial morphology.

CHROMOSOMES: We reference chromosomal information in the published literature, but also provide unpublished karyotypes for several species. Chromosomes from these samples were prepared as referenced by Patton (1967) and Gardner and Patton (1976). We use four terms to describe shape of chromosomes based on position of the centromere: **metacentric**, biarmed chromosomes with arms of nearly equal length; **submetacentric**, biarmed chromosomes with a short arm at least one-third the length of the other; **subtelocentric**, biarmed chromosomes with a short arm less than one-third the length of the other; **acrocentric** (or telocentric), chromosomes with a very minute second arm or no such discernable segment.

UNIVARIATE AND MULTIVARIATE STATISTICAL ANALYSES: We calculated standard descriptive statistics—mean, standard deviation, and observed range—for some samples. The significance of the difference between two sample means was determined by a Student's *t*-test (two-tailed). Wherever we refer to the contrast between sample means as being significant, we are rejecting the null hypothesis by using the 0.05 level of significance.

Proportional relationships between different combinations of species are illustrated by ratio diagrams. For each measurement, the absolute value of the mean, and plus or minus two standard errors of the mean, were converted to logarithms. Next, the logarithm of the mean of the standard was subtracted from the logarithms of the mean, and plus or minus two standard errors, of the comparative sample. Measurements larger than the standard are thus represented by positive values, those smaller by negative values. The solid or dashed lines in each diagram connect sample means, and the horizontal bars represent plus or minus two standard errors of the mean. A sample having the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the sample being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar.

Plottings of principal components and cluster analyses provided visual patterns that reflect similarity or contrast in the combination of all cranial and dental dimensions between geographic samples of a single species or between samples of different species. Principal components and discriminant function analyses were computed by using the combination of cranial and dental measurements indicated in various tables in the text. All measurement values were transformed to natural logarithms. Principal components were extracted from the variance–covariance matrix and loadings were expressed as Pearson product–moment correlation coefficients of the components with the original cranial and dental measurements. Canonical variates were extracted from the discriminant function analyses. Cluster analyses used the Euclidean distance measure and Mahalanobis' distances between group centroids. SYSTAT 6.0 for Windows (1996 edition) was used for all analytical procedures.

ACKNOWLEDGMENTS

We could not have completed this project without the cooperation of all the curators and supporting staff at the institutions in which we worked and from where we borrowed specimens. We greatly appreciate their unselfish efforts and the time deflected from their own responsibilities to provide access to collections and archival material as well as honor our many requests for loans of specimens. Paula Jenkins was especially patient in responding to our many requests for important samples stored in the British Museum. She also extracted trapping information from field notes made by Ian Bishop for specimens collected at Serro do Roncador; we are grateful to Bishop for allowing us access to his journal. Barbara Herzig, at the Naturhistorisches Museum Wien, loaned us specimens collected by J. Natterer and also provided related information gleaned from the archives in Wien; we could not have solved some of the nomenclatural problems without her help.

Although we collected some of the specimens used in this report (G. G. Musser in Costa Rica; M. D. Carleton in Brazil; A. L. Gardner in Costa Rica, Colombia, Venezuela, Ecuador, and Perú), many samples had been obtained on expeditions led by Sydney Anderson (Bolivia), Robert Voss (Ecuador, French Guiana, and Venezuela), Mark Engstrom (Guyana), James L. Patton (Brazil and Perú), Robert Timm and Neal Woodman (Perú), Ian Bishop (Brazil), Michael Mares and Janet Braun (Brazil and Argentina), Phil Myers (Paraguay), and Charles Handley (Panamá). Some of their expeditionary work has been published, but much has not, and contents of some unpublished results as well as ongoing research plans converged and in some cases overlapped with our interests (Voss and Myers in particular); despite this conflict, these colleagues allowed us unhindered access to any specimens (many still uncataloged) and field notes we wanted to use for our study. Mere thanks is an insufficient acknowledgment of their contributions to our research efforts. We single them out for special praise and as examples of the unselfish cooperation that is idealized but often unrealized in scientific inquiry.

James L. Patton deserves special mention. Specimens of *Oryzomys yunganus, O. capito, O, nitidus*, and *O. macconnelli* from the Rio Juruá that we studied were collected by Patton, Maria Nazareth da Silva, and Jay Malcolm as part of their Projeto Juruá, sponsored by the Conselho Nacional de Desenvolvimento Científico e Tecnológico and Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renovavais. Not only did Patton arrange to mail us hundreds of skulls, but he provided unpublished data from his chromosomal and biochemical analyses and strongly urged us to incorporate it into our report.

Illustrations were contributed by several talented artists. Most photographic prints of skulls were made by Peter Goldberg; holotypes in museums at London, Copenhagen, Berlin, and Washington, D.C. were photographed by A. L. Gardner, who also photographed most of the chromosomal spreads. Patricia Wynne prepared the line drawings in figures 2, 24, 27, 28, 29, 31, 42, 55, 56, 62, 65, 76, 77, 82, 83, and 151. Fran Stiles rendered the heads and feet in figures 53 and 54. Eric Brothers is responsible for all the other figures with line drawings, the maps, and the hind feet in figure 17. Joan Whelan produced the SEM micrographs of molar rows.

We provide English translations of several descriptions of *Oryzomys* originally published in foreign languages. German, Dutch, and Danish texts were converted by E. Brothers (Helmut Sommers checked some of Eric's translations); Azara's (1801) descriptions in French were translated by Mary Ellen Holden. The Portuguese translation of our abstract was prepared by Albert D. Ditchfield.

Robert S. Voss, James L. Patton, Philip Myers, and Victor Pacheco read the manuscript. Their critical and enlightening reviews significantly contributed to clearer transmission of our results.

DEFINITION OF THE *ORYZOMYS* ‘‘*CAPITO*’’ COMPLEX

Our understanding of this species complex is far more restricted than that intended by Hershkovitz (1960) or Cabrera (1961). We refer to a cluster containing only two entities currently recognized as *O. oniscus* and *O. capito* (Musser and Carleton, 1993). The range of morphological variation within each as well as the limits of their geographic distributions are unclear.

Neither taxon has been taxonomically re-

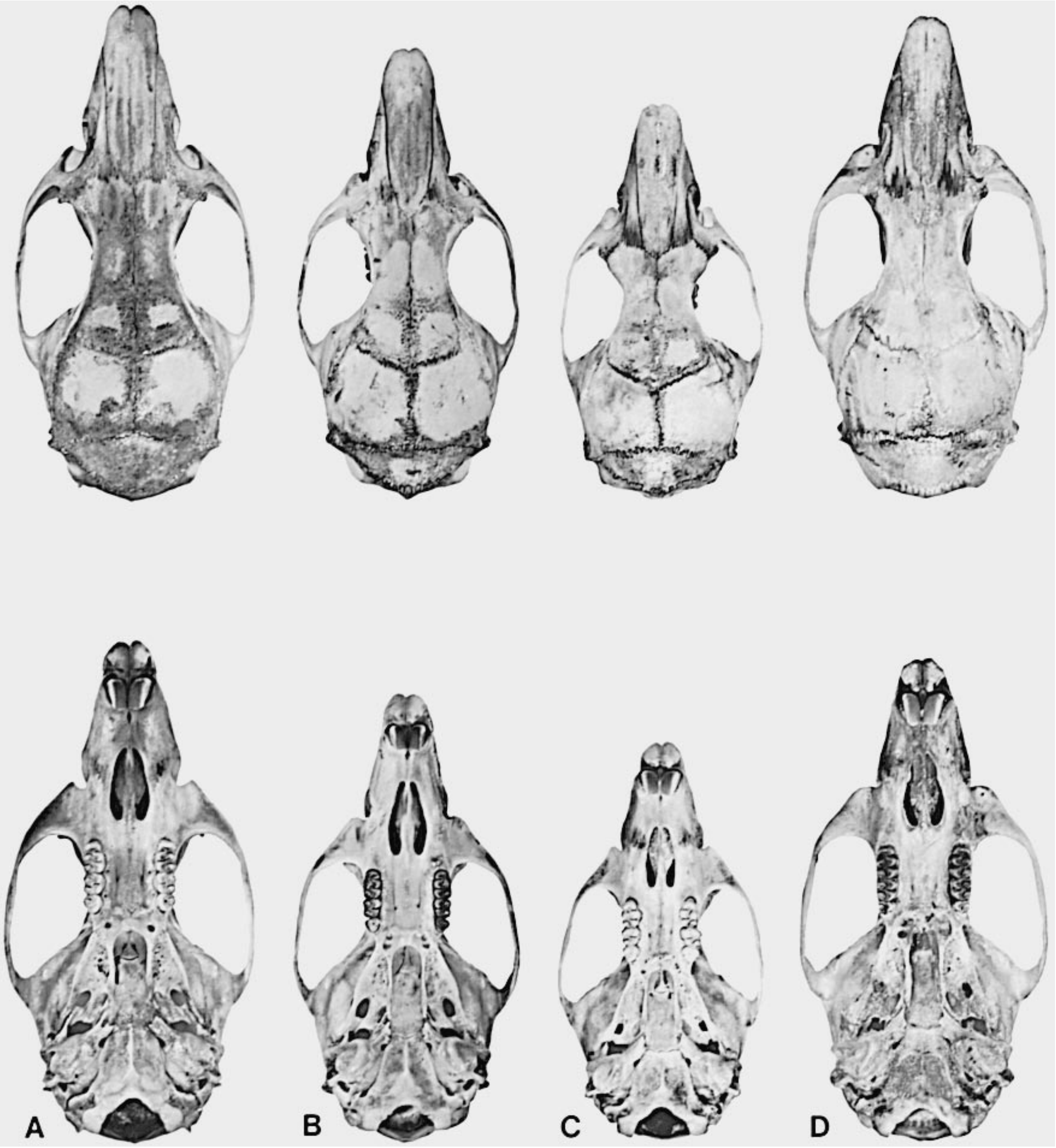

Fig. 3. Dorsal (top row) and ventral (bottom row) views of adult crania in the *Oryzomys* ''*capito*'' complex portraying variation in cranial dimensions among samples from the western region of the geographic range in Perú east to the Atlantic Forest of Brazil. **A,** AMNH 230975 from San Pablo, Departamento de Pasco, Perú, longitude 75°W (locality 46 in gazetteer for *O. yunganus*), an example of the populations from western margins of the Amazon Basin characterized by large skulls. **B,** ROM 98838 from Santa Cruz, Barima-Waini District, Guyana (sample 3 in table 1), a representative of the populations from Trinidad, the Guiana region, and eastern margins of the Amazon Basin in Brazil that contain, on the average, small animals. **C,** AMNH 96779 from Rio Tocantins, Ilha do Taiuna, Pará, Brazil, longitude 49°W (sample 41 in table 1), a specimen from populations containing the smallest animals sampled. **D,** USNM 545056 from the Atlantic Forest at Ilhéus, Bahia, Brazil, longitude 40°W (sample 45 in table 1). Crania A–C exemplify the geographic variation found in *O. megacephalus* (formerly called *capito*) as revealed by cluster and principal components analyses (figs. 4, 5); D is an example of *O. laticeps* (formerly called *oniscus*). Note that in size, D is very much like the cranium from Perú, a similarity that is also reflected in results of multivariate analyses based on cranial and dental measurements (figs. 4, 5). ×2.

TABLE 1

Population Samples of the *Oryzomys "capito"* Complex Used in the Analyses

(Each sample ranges in age from young to old adults. Descriptive statistics for each sample are listed in appendix A; specimens measured are listed in appendix B. Total *N* = 773.)

	Sample	*N*	Single or pooled localities
1.	FRENCH GUIANA	44	Arataye (03°59'N/52°34'W); Paracou (05°17'N/52°55'W); Cacao (04°35'N/52°28'W); Säul (03°37'N/53°12'W)
2.	SURINAM	7	Tafelberg (03°56'N/56°10'W); Kaiser Gebergte Airstrip (03°06'N/56°28'W)
3.	GUYANA: Barima-Waini	13	Waikerebi (07°31'N/59°23'W; Baramita, Old World (07°22'N/60°29'W); Kwabanna (07°34'N/59°09'W); Santa Cruz (07°40'N/59°14'W)
4.	GUYANA: Takutu-Essoquibo	3	30 km NE Surama (04°20'N/58°51'W)
5.	VENEZUELA: Bolívar-1	32	Auyán Tepuy (05°45'N/62°30'W)
6.	VENEZUELA: Bolívar-2	22	Arabopó (05°06'N/60°44'W)
7.	VENEZUELA: Amazonas	9	Brazo (Río) Casiquiare lowlands (250 m) at El Merey (03°05'N/65°55"W), and nearby along Río Orinoco
8.	TRINIDAD	41	Princes Town (10°16'N/61°23'W), holotype of *O. velutinus*; Bush Bush Forest, Nariva Swamp (10°24'N/61°03'W); Sangre Grande (10°35'N/61°07'W)
9.	COLOMBIA: Cundinamarca	23	Guaicaramo (04°43'N/73°02'W); Mámbita (04°46'N/73°19'W)
10.	ECUADOR: Napo + Pastaza	35	Limóncocha (00°25'S/76°38'W); San José Abajo (00°26'S/77°10'W); Avila (00°38'S/77°25'W); Río Suno Abajo (00°48'S/77°25'W); Sarayacu (01°44'S/77°29'W)
11.	ECUADOR: Zamora-Chinchipe	2	Zamora (04°04'S/78°58'W)
12.	PERÚ: Loreto	2	Huachi (03°25'S/76°20'W)
13.	PERÚ: Pasco	21	Nevati Mission, San Pablo (10°27'S/74°52'W)
14.	PERÚ: Junín	1	Perené (10°06'S/75°13'W); holotype of *O. perenensis*
15.	PERÚ: Ucayali	22	Balta (10°06'S/71°14'W)
16.	BOLIVIA: Pando-1	10	La Cruz (11°24'S/67°13'W); Independencia (11°26'S/67°34'W); Palmira (11°42'S/67°56'W); Santa Rosa (12°13'S/68°24'W); Isla Gargantua (12°23'S/68°35'W)
17.	BOLIVIA: Pando-2	1	West bank Río Beni, opposite Hamburgo (11°01'S/66°06'W)
18.	BOLIVIA: Beni	32	Río Iténez (12°29'S/64°17'W); Boca Río Baures (12°30'S/64°18'W)
19.	BOLIVIA: Cochabamba	2	2 km E Cochabamba (16°57'S/65°23'W)
20.	BOLIVIA: Santa Cruz	10	Río Mamorae, 2 km N de la boca del Río Chapari (15°57'S/64°41'W); 4.5 km N, 1.5 km E Cerro Amboro, Río Pitasama (17°45'S/63°40'W); 2 km SW Las Cruces (17°47'S/63°22'W); 3 km N San Rafael de Amboro, Río Saguayo (17°34'S/63°42'W); San Rafael de Amboro (17°36'S/63°36'W)
21.	BRAZIL: Acre-1	5	Km 8 on Route BR 364 between Sena Madureira and Manuel Urbano (09°05'S/68°41'W)
22.	BRAZIL: Acre-2 (left bank Rio Juruá)	20	Opposite Igarapé Porongaba (08°40'S/72°47'W)
23.	BRAZIL: Acre-3 (right bank Rio Juruá)	21	Igarapé Porongaba
24.	BRAZIL: Acre-4 (left bank Rio Juruá)	5	Sobral (08°22'S/72°49'W)

TABLE 1
(Continued)

Sample	*N*	Single or pooled localities
25. BRAZIL: Acre-5 (right bank Rio Juruá)	7	Nova Vida (08°22'S/72°49'W)
26. BRAZIL: Amazonas-1 (left bank Rio Juruá)	15	Seringal Condor (06°45'S/70°51'W)
27. BRAZIL: Amazonas-2 (right bank Rio Juruá)	17	Sacado (06°45'S/70°51'W)
28. BRAZIL: Amazonas-3 (right bank Rio Juruá)	29	Penedo (06°50'S/70°45'W)
29. BRAZIL: Amazonas-4 (left bank Rio Juruá)	18	Igarapé Nova Empresa (06°48'S/70°44'W)
30. BRAZIL: Amazonas-5 (left bank Rio Juruá)	35	Opposite Altamira (06°35'S/68°54'W); Barro Vermelho (06°28'S/58°46'W)
31. BRAZIL: Amazonas-6 (right bank Rio Juruá)	26	Altamira; Jainú (06°28'S/68°46'W)
32. BRAZIL: Amazonas-7 (left bank Rio Juruá)	24	Colocação Vira Volta (03°17'S/66°14'W)
33. BRAZIL: Amazonas-8 (left bank Rio Juruá)	13	Ilhazina, Vira Volta (03°17'S/66°14'W)
34. BRAZIL: Amazonas-9	2	80 km N Manaus (02°25'S/59°50'W)
35. BRAZIL: Mato Grosso	26	Serra do Roncador, 264 km (by road) N Xavantina (12°49'S/51°46'W)
36. BRAZIL: Goiás	11	Anápolis (16°20'S/48°58'W)
37. BRAZIL: Federal District	10	20 km SW, 20 and 25 km S Brasilia (15°57'S/47°54'W; Mares et al., 1989:7)
38. BRAZIL: Pará-1	29	Km 200 and km 212 S Itaituba between Itaituba and Jacaréacanga on the Trans-Amazonian Highway on left (west) bank of Rio Tapajós (04°–06°S/56°–58°W)
39. BRAZIL: Pará-2	16	Km 19 S Itaituba between Itaituba and Jacaréacanga on the Trans-Amazonian Highway; km 25 between Itaituba and Altamira on highway BR 230, Rio Tapacurazinho; Itaituba, Rio Tapajós (04°17'S/55°59'W), holotype of *O. goeldi*
40. BRAZIL: Pará-3	9	18 km S, 19 km W Altamira (Agrovila da Uniao), km 43 on Trans-Amazonian Highway between Itaituba and Altamira (03°22'S/52°35'W)
41. BRAZIL: Pará-4	36	Near Rio Xingu: Vilarinho do Monte (01°37'S/52°01'W); Recreio at Majahry (01°42'S/52°12'W); Rio Tocantins, Ilha do Taiuna (02°15'S/49°30'W); Capim, km 93 and km 94 on Route BR 14 (01°41'S/47°44'W); Belém, Utinga (01°27'S/48°29'W); 150 mi SE Belém
42. BRAZIL: Amapá	44	Serra do Navio, Serra C3 (00°59'N/52°03'W)
43. PARAGUAY	13	SW Cerro Corá (25°15'S/55°59'W; 28 km SW Pedro Caballero; 13.3 km (by road) N Curuguaty (24°31'S/55°42'W)
44. BRAZIL: Pernambuco	4	São Lourenço da Mata, 10 km WNW Recife (08°00'S/35°03'W); includes holotype of *O. oniscus*
45. BRAZIL: Bahia	3	Ilhéus (14°49'S/39°02'W); 37 km N, 34 km E Jequié (13°51'S/40°05'W)
46. BRAZIL: Espírito Santo	3	Conceição da Barra (18°35'S/39°45'W); Santa Cruz (19°56'S/40°09'W)

vised, nor do we present a revision here. However, in the process of sorting hundreds of museum specimens into *yunganus, nitidus, russatus* (formerly *intermedius*), *macconnelli, talamancae, bolivaris,* or the other two species we describe as new, we necessarily identified members of our ''*capito*'' complex from throughout most of its geographic range. In working with examples of this complex, we perceived a conspicuous range in body and cranial size roughly associated with geography: large animals occur in the western parts of its range; small body size is typical in the northern segment, in the eastern regions of the Brazilian states of Mato Grosso and Pará, and in eastern Paraguay; and farther east and southeast in Brazil, samples from Pernambuco, Bahia, Espírito Santo, and Minas Gerais are again characterized by large body size. The striking variation in overall cranial dimensions can easily be seen in figure 3: a cranium from Perú represents the large-bodied populations in the western portions of the Amazon Basin, examples from Guyana and Pará portray the smaller bodied populations from the Guiana Region and eastern part of the Amazon Basin, respectively, and a specimen from Bahia typifies samples from the Atlantic region in Brazil. The populations from Pernambuco and Bahia are usually considered a separate species, *O. oniscus*; those from the Guiana Region and Amazon Basin, the broad expanse of tropical lowland evergreen forest generally referred to as Amazonia (Haffer, 1987), are currently identified as *O. capito* (Musser and Carleton, 1993).

ANALYTICAL SAMPLES AND VARIATION PATTERNS

We needed to quantify the pattern of the exceptional variation among samples and to determine its possible significance for delineating species within the complex by using the kinds of data (primarily morphological) available to us. Readers would then know our concept of *O. capito,* an understanding of which is critical to defining the species upon which our report focuses: *yunganus, bolivaris, talamancae, nitidus, macconnelli, russatus,* and two undescribed taxa. Specimens of all have at one time or another been identified as *O. capito* or some other taxon in the ''*capito*'' complex. To delimit their morphological and geographic boundaries logically requires comparison with species that we regard as the ''*capito*'' complex, particularly with what is currently recognized as *O. capito.* Thus, formulating definitions of that species and possibly others in the ''*capito*'' complex based on some objective suite of characters (primarily morphological in this case) and identifying the correct scientific names for them, form a necessary prelude to our accounts of the species formerly associated with the *O.* ''*laticeps*'' or ''*capito*'' complex of other authors (Tate, 1939; Hershkovitz, 1959; Cabrera, 1961).

We studied and measured 773 crania from 46 geographic samples within the known geographic range of what has been called *O. capito* and *O. oniscus*: Amazonia (see map of Amazonia in fig. 15), eastern Paraguay, and the Atlantic Forest and adjacent areas of eastern Brazil. Contents of those samples are described in table 1, descriptive statistics for each are listed in appendix A, and the specimens measured are identified in appendix B. We did not include lengths of head and body, tail, hind foot, or ear in the 46 samples. Such data are unavailable for many samples consisting only of skulls; for others, it is impossible to know whether variability in external measurements reflects actual population variation or the differing abilities of so many collectors to obtain accurate values.

Geographic variation among samples is summarized in a cluster diagram (fig. 4) and results of principal components analyses (figs. 5, 12). We consider the patterns in the diagram and plots only rough estimates of morphometric similarities and differences because they are based only on specimens readily available to us. Sample sizes are uneven (ranging from 1 to 44; table 1), and those consisting of more than one specimen may contain different age combinations of young to old adults. Finally, our geographic sampling is unequal. We were able to obtain measurable series of specimens from most of the known distribution of our *O.* ''*capito*'' complex, but vast regions of the range are unrepresented. Sampling is most dense along the western portion of the Amazon Basin; about one-third of the total specimens mea-

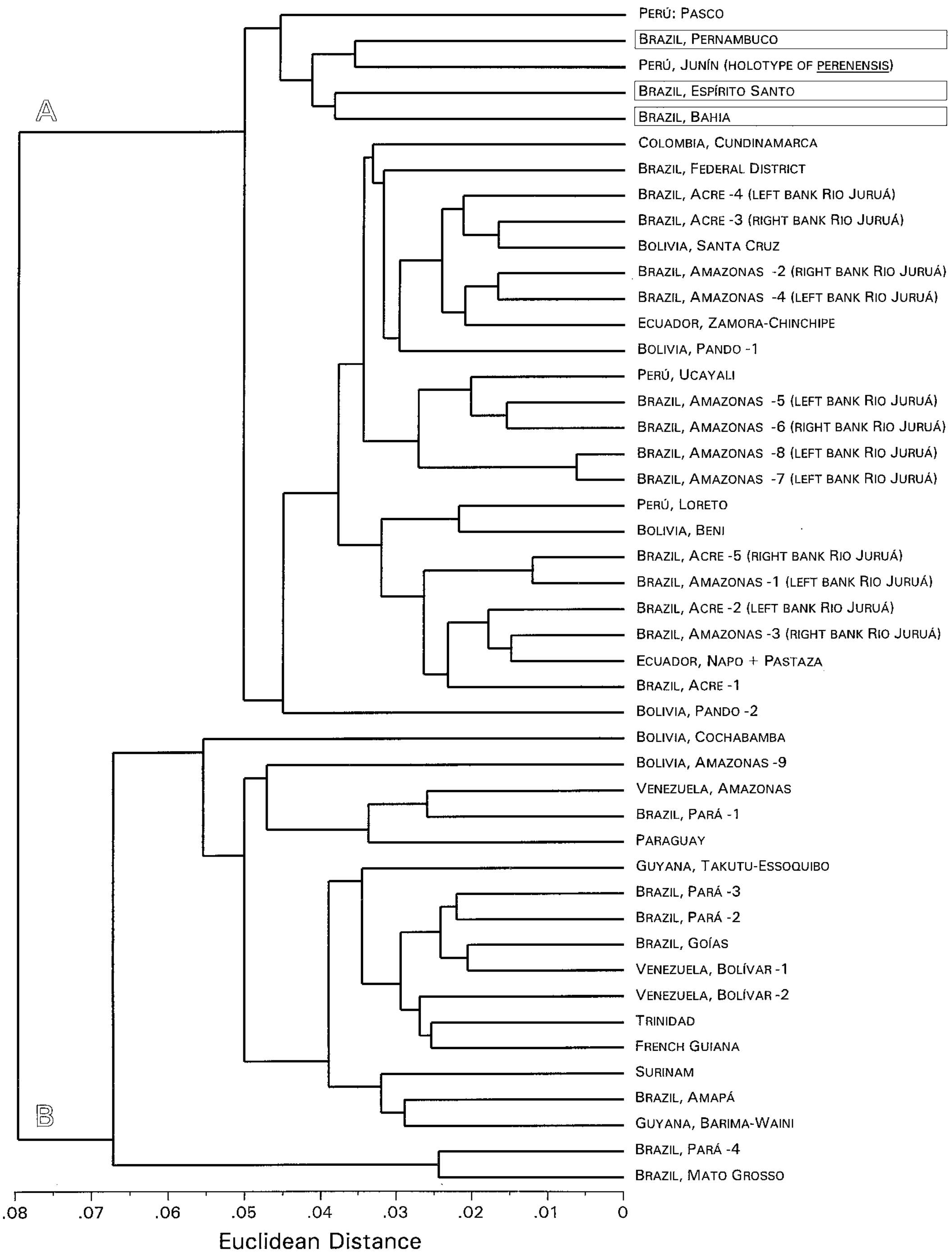

Fig. 4. UPGMA cluster diagram using Euclidean distance derived from log-transformed means of 13 cranial and 2 dental variables (listed in appendix A) for the 46 samples (identified in table 1) representing the *Oryzomys* "*capito*" complex. Boxes enclose Atlantic Forest samples.

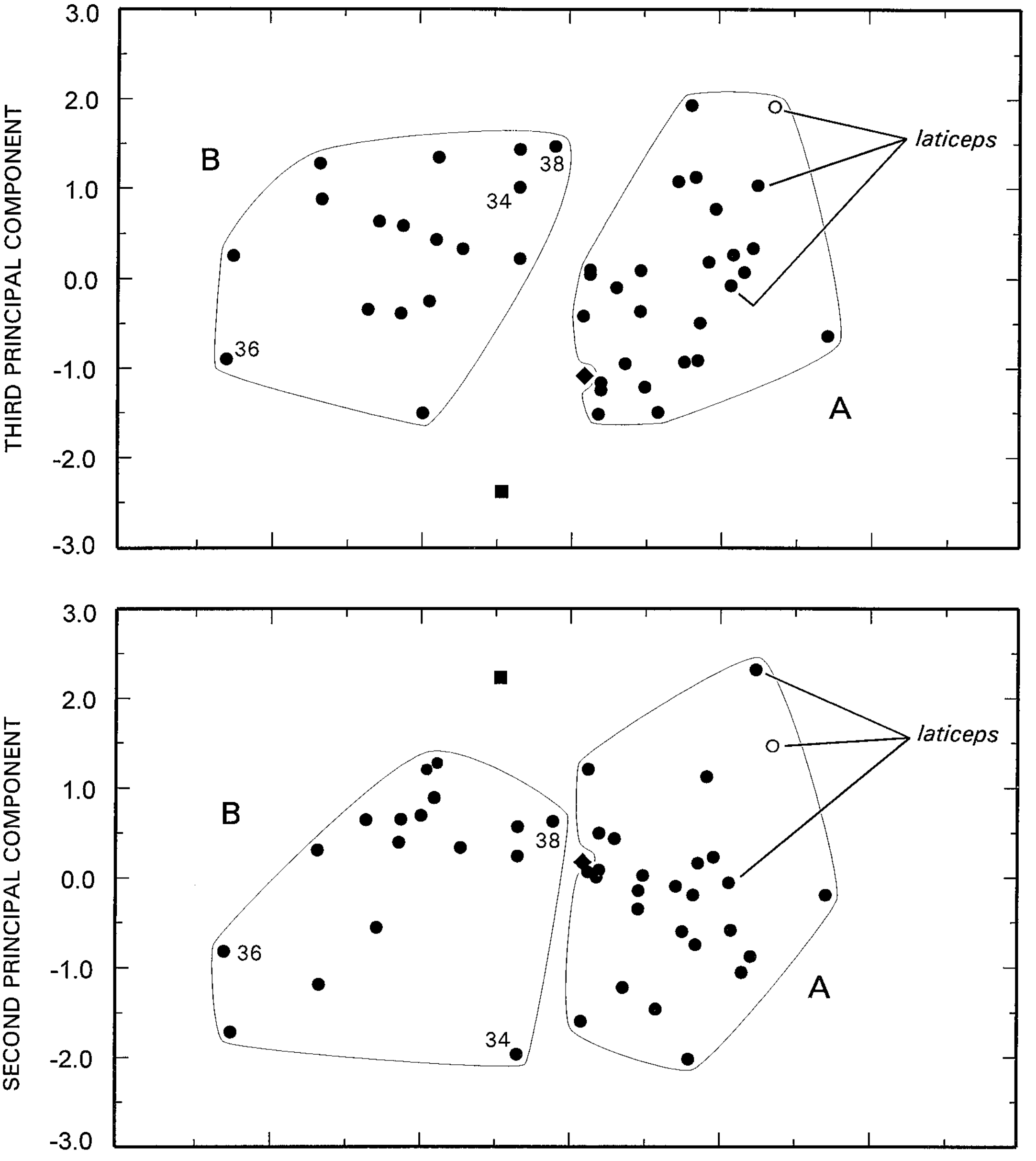

Fig. 5. Sample scores, based on log-transformed mean values of 13 cranial and 2 dental variables (see table 2), projected onto the first, second, and third principal components extracted from analysis of adults in the 46 samples listed in table 1. Leaders point to samples 44–46 (table 1) from the Atlantic Forest that we identify as *O. laticeps* (formerly called *oniscus*); circle represents mean score of four specimens from the type series of *oniscus* forming sample 44. All other plots represent *O. megacephalus*.

Enclosed data points in the right half of upper and lower plots (**A**) represent populations from western segment of the Amazon Basin (Ecuador, Perú, Bolivia, and western Brazil) that are characterized by large body size (samples 9–18, 20–33; table 1); these same samples cluster to form the largest of the

TABLE 2
Results of Principal Components Analysis of Cranial and Dental Means of Forty-six Samples of the *Oryzomys* "*capito*" Complex
(Mean values for variables in each sample listed in appendix A; specimens measured identified in appendix B. See fig. 5.)

	Principal components		
Variable	First	Second	Third
ONL	0.042	–0.001	–0.003
ZB	0.043	–0.002	–0.001
IB	0.023	0.007	–0.008
LR	0.039	0.005	0.008
BR	0.041	0.003	0.011
LB	0.035	0.001	–0.004
HBC	0.036	–0.004	–0.012
BZP	0.067	–0.017	0.005
LD	0.049	–0.012	0.004
LBP	0.052	–0.006	–0.009
PPL	0.039	–0.004	0.011
LIF	0.029	–0.006	0.013
BIF	0.010	–0.033	0.015
CLM1–3	0.039	–0.013	–0.010
BM1	0.044	0.013	–0.019
Eigenvalue	0.027	0.002	0.002
% Variance	75.9	5.7	4.4

sured, for example, were collected along the Rio Juruá in western Brazil.

Cluster and principal components analyses reveal a pattern of variation in cranial and dental measurements that reinforces our initial visual perception of that variation as we sorted specimens. Populations of larger bodied animals (we assume that overall cranial dimensions generally reflect body size) are found in the western portion of the Amazon Basin. Smaller body size, on average, characterizes most populations in the central and eastern part of the Basin, southern Venezuela, eastern Paraguay, the Guiana Region (including the tepuis of eastern Venezuela), and Trinidad. Finally, specimens in samples from the Atlantic region of Brazil are more similar in cranial size to samples from the western part of the Amazon Basin than they are to the smaller animals from the eastern rim of the Basin and from eastern Paraguay.

Results of cluster analyses of sample means (fig. 4) graphically portray the pattern of variation among samples traditionally identified as *Oryzomys capito* and *O. oniscus.* Two primary clusters are conspicuous. Except for four samples, the larger cluster (A) represents approximately the western half of the Amazon Basin. The actual samples originated from west-central and northwestern Bolivia, Perú, the adjacent states of Acre and western Amazonas in Brazil, Ecuador, and the eastern Andean foothills of Colombia. Specimens of large body size are common to these samples from western Amazonia, as is indicated by the means (appendix A). For example, the range in mean values for occipitonasal length is 32.3–35.0 mm, and for crown length of upper molars is 4.8–5.3 mm.

Three of the four exceptions previously mentioned are those samples (44–46, table 1) from the Atlantic Forest of eastern Brazil in the states of Pernambuco, Bahia, and Espírito Santo that are usually identified as *O. oniscus* (see Musser and Carleton, 1993). Large body size is a primary defining trait of *oniscus* and this aspect, as indicated by cranial and dental measurements (see appendix A), is reflected in the cluster diagram. The type series of *oniscus* from Pernambuco, as well as the samples from Bahia and Espírito Santo (three specimens in each), contains, on

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←

two primary assemblages (A) in figure 4. Samples from this geographic region revealed a common genic signature (fig. 6) and diploid number of chromosomes ($2n = 52$; table 13). Data points encircled in the left half of each plot (**B**) designate populations in Trinidad, Venezuela, Guiana region, central and eastern margins of the Amazon Basin, and eastern Paraguay that are characterized by small cranial dimensions (samples 1–8, 34–36, 38–43; table 1); these population samples cluster to form the smaller of the two primary groups (B) in figure 4. Specimens from this eastern geographic area yielded different genic traits (fig. 6) and diploid number ($2n = 54$; table 13) than did those obtained in western Amazonia. The black square designates mean score for Bolivian sample 19 from Cochabamba, the black diamond indicates the mean score for sample 37 from the Federal District of Brazil, and the numbered scores refer to particular samples discussed in text (34 = Manaus, 36 = Anápolis, 38 = left bank Rio Tapajós).

average, some of the largest animals sampled and nest (fig. 4) with two Peruvian series that are also characterized by large cranial and dental measurements (appendix A).

The fourth exception is sample 37 (table 1) from the Federal District of Brazil, south and southwest of Brasilia. We discuss its significance farther on in the account.

The second major cluster (B) in figure 4, with one exception, was derived from samples collected over a broad area nestled between western Amazonia and the Atlantic Forest: the Guiana Region, southern drainage of Río Orinoco, central and eastern portions of the Amazon Basin, and eastern Paraguay. In the north, specimens come from eastern Bolívar and Amazonas in Venezuela, the island of Trinidad, northern Guyana, Surinam, and French Guiana. To the south, samples are from Brazil in Amapá, eastern Amazonas, western to eastern Pará, Goiás, southeastern Mato Grosso, and eastern Paraguay. Small body size sets these samples apart from specimens in the other cluster; for example, ranges of sample means for occipitonasal length and crown length of molar row are 28.9–32.5 mm and 4.3–4.9 mm, respectively (see descriptive statistics in appendix A).

The single geographic exception is Bolivian sample 19 from Cochabamba (table 1; fig. 4), which consists of two old adults. We expected that means of their measurements would cluster closer to other Bolivian samples contained in the first primary cluster rather than in the second. Both specimens have small skulls, which is typical of animals from central and eastern Amazonia, but they also possess long molar rows, a trait characteristic of the other Bolivian samples from western Amazonia (see appendix A). More specimens from the Cochabamba region are needed to assess the significance of the morphometric variation evident in our present small sample.

Principal components analysis of the 15 mean cranial and dental dimensions for all 46 samples (table 1) reinforces the morphometric relationships illustrated in the cluster diagram. Sample mean scores are scattered along the first principal component (fig. 5); dispersion is strongly influenced by variation in nearly all cranial and dental measurements (table 2), which reflects variation in overall size. Separation of plots along the second component is strongly influenced only by variation in breadth of incisive foramina, but covariation of many variables (breadth of first upper molar, breadth and length of incisive foramina, height of braincase, for example) accounts for the spread of scores along the third principal component. Scores representing samples from the western portion of the Amazon Basin, as well as those samples from the Atlantic Forest of eastern Brazil in Pernambuco, Bahia, and Espírito Santo, form the right aggregation (A) in the upper and lower diagrams and are comparable to contents of the larger primary cluster (A) in figure 4. Those points designating samples from the Guiana Region, southern Venezuela, eastern portions of the Amazon Basin in Brazil, and eastern Paraguay lie to the left (B) and represent the same samples in the smaller second assemblage (B) in the cluster diagram (fig. 4). Separation between the groups is more evident in the upper principal components diagram (fig. 5).

The similarity in cranial dimensions between the three samples from the Atlantic Forest and those collected in the western portion of the Amazon Basin is strikingly revealed by the principal components analysis (fig. 5). The position of specimens from Pernambuco, Bahia, and Espírito Santo, in both the cluster pattern and principal components scatterplot, corroborates our initial conclusions derived from visual inspection of crania: in morphology and body size they closely resemble specimens from western regions of the Amazon Basin in Bolivia, Perú, and western Brazil, among which are some of the largest crania surveyed (fig. 3). Without the Atlantic Forest provenance of the Brazilian animals, we would have unhesitatingly identified them as coming from western Amazonia.

Other kinds of data, although scanty from incomplete sampling, seem to coincide with results of our analysis of geographic variation within the *O.* ‘‘*capito*’’ complex. In this context, J. L. Patton generously provided us with results obtained by him and M. N. da Silva from analyses of limited sequence data (sequence variation in base pairs of the mitochondrial cytochrome-b gene) from samples of the *O.* ‘‘*capito*’’ complex and urged

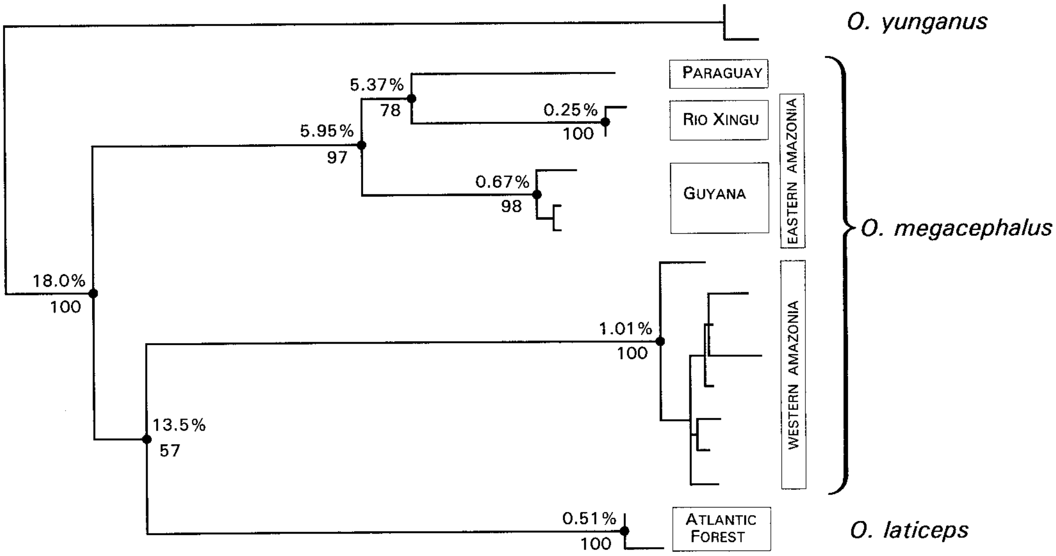

Fig. 6. Consensus tree of 251 minimal length trees based on maximum parsimony analysis of 401 base pairs of the mitochondrial cytochrome-b sequence (see Patton et al., 1996) for members of the *Oryzomys* "*capito*" complex (tree length = 172 steps, CI = 0.733, RI = 0.891, RC = 0.653). Average percent sequence divergence (Kimura 2-parameter estimates) is given above the nodes, and bootstrap values (from 100 replicates) are indicated below nodes. Tree was rooted by comparison to an outgroup comprised of *O. macconnelli*, *O. nitidus*, and *O. russatus*. Individual haplotypes (specimens) are listed below following order of terminal twigs from top of the tree down:

O. yunganus

1. Brazil: MNFS 1101; Porongaba, right bank Rio Juruá, Acre.
2. Brazil: JLP 15535; Condor, left bank Rio Juruá, Amazonas.

O. megacephalus—Eastern Amazonia and eastern Paraguay

3. Paraguay: Specimen reported by Myers et al. (1995).
4. Brazil: USNM 549547; Altamira, Rio Xingu, Pará.
5. Brazil: USNM 549548; Altamira, Rio Xingu, Pará.
6. Guyana: ROM 31091.
7. Guyana: ROM 31092.
8. Guyana: ROM 33480.

O. megacephalus—Western Amazonia

9. Perú: MVZ 166676; Kiteni, Río Alto Urubamba, Cuzco (the other sequence used by Myers et al., 1995; originally from Smith and Patton, 1993).
10. Brazil: MNFS 1100; Porongaba, right bank Rio Juruá, Acre.
11. Brazil: JLP 15758; Jainú, right bank Rio Juruá, Amazonas.
12. Perú: MVZ 154944; Huampami, Río Cenepa, Amazonas.
13. Brazil: JUR 551; Ilhazinha, left bank Rio Juruá, Amazonas.
14. Brazil: MNFS 1586; Nova Vida, right bank Rio Juruá, Acre.
15. Brazil: JLP 15968; Altamira, right bank Rio Juruá, Amazonas.
16. Brazil: JLP 15311; Penedo, right bank Rio Juruá, Amazonas.

O. laticeps—Atlantic Forest

17. Brazil: EDH 22; Itabuna, 25 km W Ilhéus, 600 m (13°32′S/39°16′W), Bahia.
18. Brazil: ML 101; Itabuna, 25 km W Ilhéus, 600 m (13°32′S/39°16′W), Bahia.

that we include it here, which we have done in figure 6. In Patton's words (personal commun.; letter in AMNH Mammalogy Archives),

> Amazonian "*capito*" is deeply divided into western and eastern mtDNA clades. Our samples are too inadequate geographically to determine if these entities overlap somewhere in the central Amazon. While there is a clear need for serious sampling in the cen-

> tral portion of the basin between the eastern and western groupings, to me there is a clearly emerging pattern of congruence between the limited sequence data and what you all are seeing in morphometric trends. This congruence suggests to me that there are two distinct taxa of *capito* in Amazonia, the geographic boundaries of which are still fuzzy (but with a dividing line somewhere along the Río Madeira–Río Negro axis, or somewhat to the east) . . . coastal Brazilian *laticeps*, while it clusters closer to western Amazonian ''*capito*'', really is about equidistant to the two Amazonian clades, all of which differ by a substantial degree (13-14% sequence divergence is an enormous value).

That different groups existed based on variation in sequence data had already been suggested by Myers et al. (1995: 375) in a study designed to investigate phylogenetic relationships among particular taxa of South American muroids as indicated by cytochrome-b sequences. Myers and his collaborators recorded substantial genetic distance between a specimen of ''*capito*'' from Perú and one from Paraguay: the ''DNA . . . differed at 50 sites (12.5%),'' and a ''relatively high percentage of the differences . . . were transversions.'' The differences appeared anomalous compared to those of lesser magnitude found between conspecific populations of the other oryzomyines they sampled. Patton (personal commun.; letter in AMNH Mammalogy Archives) incorporated the 401 bp sequence from the specimen used by Myers et al. (1995) in his analyses of samples from Perú, Guyana, and Brazil, producing the results depicted in figure 6. Patton wrote that the ''Paraguay specimen clearly and closely associates with the eastern Amazonian group (bootstrap value of 97%), not with '*laticeps*' [coastal Brazilian sample] or western '*capito.*' The Paraguay specimen also fits with the sample from the Rio Xingu, although not with great confidence (bootstrap value of only 78%).''

Documented chromosomal variation (table 13) seems to mirror results from morphometric and sequence analyses. Samples of the western populations from Ecuador, Perú, and western Brazil along the Rio Juruá are characterized by a diploid number of 52, as are samples from the states of Paraíba and Pernambuco in the Atlantic Forest of coastal northeastern Brazil. In contrast, the 2*n* is 54 in samples from Venezuela, Surinam, central Brazil (Manaus, Rio Xingu, Federal District), and Paraguay, regions where smaller body size prevails.

We interpret the geographic pattern of morphometric variation described above to represent two species. One consists of populations from Amazonia and eastern Paraguay, for which the oldest name is *O. megacephalus* (formerly called *capito*); the other is represented by samples from the Atlantic Forest and adjacent regions in eastern Brazil, for which *O. laticeps* (formerly known as *oniscus*) is the correct name (we defend our use of these names later in each account).

NOMENCLATURAL CONSIDERATIONS

The earliest description of a member of the ''*capito*'' complex is attributed to Felix de Azara. His ''Essais sur l'histoire naturelle des quadrupèds de la province du Paraguay'' was published in 1801 and in it he described the ''Rat second, ou Rat à grosse tête'' (pp. 82–85); we insert here a version in English of Azara's account (translated by M. E. Holden; the description in French, which was originally translated from Spanish by M. L. E. Moreau-Saint-Méry, is reproduced in appendix I; our notes are in brackets):

SECOND RAT OR BROAD-HEADED RAT

This species appears to be new

> It is not a precise proper name, and I do not know the feature that can best characterize this animal that I have here named.
>
> Two Indians from the village of Saint-Ignace-Gouazou[a] sold to me, on different days, two females similar to each other, without giving me any other information, whether or not they were captured in their *chacras* [gardens or croplands], or whether the plough had uncovered the refuge of these animals. I compared them with a common rat, that I am now holding for this purpose, and it appears to me that the two females are adults.
>
> Length, 8 inches (21 and $\frac{3}{5}$ centimeters).
>
> Tail, 4 inches (11 centimeters) completely hairless, except for $\frac{3}{16}$ inch (6 millimeters) at its base; a bit larger at its base, yet it does not taper as rapidly as in the ordinary rat, which is sharply pointed up to the tip.
>
> Although everything regarding the shape of this animal is similar to that of the rat, it has a much stouter and shorter head; the eye is smaller and not as prominent; the ear is much shorter, with a length of $\frac{6}{16}$ inches (1 $\frac{1}{3}$ centimeters) above the head; width of $\frac{6}{16}$ inches (1 $\frac{1}{3}$ centimeters) also, and more rounded; the whiskers are much more slender and shorter; the cheeks are stouter, and bulge outward, which ren-

ders the head nearly as large as the body; the distance is less between the eyes, and greater between the ears than in the rat. The hind legs, compared to the front, are longer; the hind foot is much larger, and is $^{13}/_{16}$ inches (3 centimeters) long, including the claws; the tail is more pitted, less wiry, and originates on a less rounded rump.

In the front paw, there are the same four fingers and the same rudimentary thumb as in the rat, with a similar arrangement; a similar situation is shown in the digits of the hind foot.

From the snout to the tail, the animal is brown; the sides of the body and those of the head are paler but very bright, with a somewhat cinnamon hue.

Three days before, an Indian from the same village sold me a rat, taken in his *chacra,* and told me that the small animal was one of four others who struck him to be of equal size, and with yet another larger one, but they all escaped. This circumstance makes me believe that the one I bought was not an adult, although to me its testicles appeared very large for this young individual. Here I describe it, having in front of me a small common rat.

It [head and body] is 5 inches (13 and $^1/_2$ centimeters) long; and like the tail is proportional to that of the broad-headed rat, that I described above, and everything regarding their shapes are similar, and I have little doubt that this is but a small individual of the current species; and as a consequence I place below the comparison that I make of the young broad-headed rat with the young common rat.

The young broad-headed rat, has a much stouter head, and the distance between the ears is larger; the face is not as flat, and the snout is not as pointed, nor as long, nor as tapered.

The fur, from the nose to the top of the head, is not as flattened; the whiskers are shorter, projecting out less.

The eye and ear are smaller; the latter is more close, thick, upright and has several small hairs in front; it extends beyond the head by $^4/_{12}$ inches (9 millimeters); it has a width of over $^3/_{12}$ inches (6 millimeters), and is rounded at its tip.

The tail is narrower at its base, and originates on a less rounded rump.

The testicles are like those of the common rat, with a length of $^4/_{12}$ inches (9 millimeters), and a width of $^2/_{12}$ inches (over 4 millimeters).

All of the inferior parts are whitish, and do not reflect the chestnut of the small common rat, and all of the upper parts and the sides, have a lead hue, darker than that of the small common rat.

[a] A place around 34 and $^1/_2$ leagues[13] (19 *myriamètres* [190 km]) in the south-quarter-southeast [south-southeast] of the city of Assumption [=Asunción]. (*Translator's note* [M. L. E. Moreau-Saint-Méry].). [There is a San Ignacio Guazú about 190 km SSE of Asunción in Departamento Misiones, southern Paraguay; see Paynter, 1989:41.]

Azara did not apply a Linnaean binominal to the animal he described, but between 1814 and 1819 three authors gave genus and species name combinations to Azara's ''Rat second, ou Rat à grosse tête.'' The oldest is *Mus megacephalus,* used by Fischer in 1814 (vol. 3, p. 71): ''*M. megacephalus,* Rat à grosse tête, d'Azara. l.c. p. 82.'' This name, as well as others coined by Fischer for the muroid rodents described by Azara (''*Mus tarso nigro,* ''*Mus Laucha* et *Lauchita,*'' ''*M. auritus,*'' and ''*M. Angouya,*'' all on p. 71), was long overlooked and has not been used as a senior synonym since it was proposed. Langguth (1966) petitioned the International Commission on Zoological Nomenclature to place *megacephalus* and five other names of Fischer on the Official List of Specific Names in Zoology. As no action was taken by the Commission, Langguth's application eventually lapsed. In the meantime, *megacephalus* and some of Fischer's other Linnaean names continue to be ignored by researchers for two primary reasons (see Myers and Carleton, 1981: 12). First, investigators following the 1961 version of the Code (or the 1970 modification) treated *megacephalus* as a ''forgotten name'' (article 23b) because it has not been used as a senior synonym for more than 50 years (Myers and Carleton, 1981: 12). Second, Sabrosky (1967: 141) noted that Fischer's work may not be valid because he did not consistently use binominal nomenclature as demanded by article 11c (in both 1961 and 1985 editions of the Code). Fischer, as interpreted by Sabrosky, may not have intentionally created formal Latin scientific names but ''was listing names from the literature, and for d'Azara he was translating them directly into Latin. . . . It is true that they are italicized, but that was his format for the names referred to, regardless of language or form.'' Sabrosky also pointed out that ''in a synopsis at the beginning of the volume, Fischer sometimes uses different names than in the text.'' These problems with Fischer's work prompted Myers and Carleton to reject one of Fisher's names, *Mus tarso nigro,* as invalid and to accept Olfers' (1818) *nigripes* as the appropriate name for the large-bodied species of *Oligoryzomys* in Paraguay.

It is regrettable that Langguth's (1966) petition received no action by the Commission. We looked at Fischer's work and reexamined the two primary reasons researchers have ignored Fischer's names: (1) status as a forgotten name and (2) inconsistent usage of binomial nomenclature—within the context of the third edition of the International Code of Zoological Nomenclature (1985).

1. Prior to the third edition, article 23b, either as worded in the 1961 edition or modified under declaration 43 published in 1970, declared that a ‘‘name that is in general current use and has been available for at least 50 years shall not be displaced after 1960 by an unused senior synonym’’ and is, among other limitations listed, to be ‘‘termed a nomen oblitum’’ [forgotten name] (International Commission on Zoological Nomenclature, 1970: 135). For a forgotten name to become available would require approval from the Commission.

Article 23b was modified in the third edition of the Code to read as follows:

> The Principle of Priority is to be used to promote stability and is not intended to be used to upset a long-accepted name in its accustomed meaning through the introduction of an unused name that is its senior synonym. An author who considers that the application of the Principle of Priority would disturb stability or universality or cause confusion is to maintain existing usage and refer the case to the Commission for a ruling. . . .

This new version leaves usage of a nomen oblitum up to the researcher, but still requires application to the Commission if such a name is to be used.

2. The third edition of the Code, as explained in article 11c, retains the requirement of binominal nomenclature for a name to be available: ‘‘The author must have consistently applied the Principle of Binominal Nomenclature . . . in the work in which the name or nomenclatural act is published.’’ A provision (iii) of this Article is relevant to judging the availability of Fischer’s names:

> An index published before 1931 in a work that is not consistently binominal is acceptable itself as a work consistent with the principle of Binominal Nomenclature provided that the Principle is consistently applied to scientific names in the index; thus a scientific name published in such an index is available if the name satisfies the other provisions of this Chapter and of Artiles 4, 5, and 6, and if there is an unambiguous link between the entry in the index and the description, illustration, or indication in the text.

None of Fischer’s names based on Azara are found in the index to vol. 3 (vols. 1 and 2 have their own respective indices). But the names are listed on page VII in a prepage section (pp. I–XXIV) to volume 3 titled ‘‘Elenchus Voluminis Tertii Zoognosiae’’ [A Review or Contents of the Third Volume of Zoognosiae] under the genus *Mus*: *nigritarsis*, *Laucha*, *auritus*, *Angouya*, and *megacephalus*. Here, Fischer formed appropriate Linnaean binomials, and he uniformly used binominal nomenclature throughout the ‘‘Elenchus.’’ In the body of volume 3, however, he inconsistently cited names based on Azara’s descriptions and used ‘‘*Mus tarso nigro*’’ and ‘‘*Mus Laucha* et Lauchita’’; whether Fischer intended, as Sabrosky (1967) suggested, only to translate Azara’s names directly into Latin is unknown. So, although binomial nomenclature in consistently employed in the ‘‘Elenchus,’’ it is not in the main body of the volume, and viewed as a whole, Fischer inconsistently used binomial nomenclature in the ‘‘Zoognosiae.’’ If the ‘‘Elenchus’’ is not interpreted as being an index, which Fischer apparently did not intend because at the end of the ‘‘Elenchus’’ he indicated that the indices began on page 695, then according to article 11c, Fischer’s names are unavailable.

But the definition of index can be broadly interpreted. In *Webster’s New Unabridged International Dictionary*, second edition, the many meanings associated with ‘‘index’’ include ‘‘table of contents,’’ ‘‘preface,’’ or ‘‘prologue.’’ Any of those terms would describe the ‘‘Elenchus.’’ Furthermore, each genus in the ‘‘Elenchus’’ is uniquely numbered and can be located in the main body by searching for that number. ‘‘*Mus*,’’ for example, is number 29 and can be located in the body of the volume by searching for 29, where under that genus are listed Fischer’s names, each clearly attributed to Azara’s description. The ‘‘Elenchus’’ seems to us to be another kind of index wherein the names listed are in the proper binomial form.

Finally, Fischer’s bibliographic reference to Azara’s work does satisfy one requirement of availability as defined in article 12a: ‘‘To be available every new scientific name published before 1931 must satisfy the provisions of Article 11 and must have been accompanied by a description or a definition of the taxon that it denotes, *or by indication*.’’ And in article 12b(1), the Code denotes ‘‘indication'' to mean ''a bibliographic reference to a previously published description or definition even if contained in a work published before 1758 *or that is not consistently binominal*.'' Five other denotations are listed but the first is the most relevant to our discussion.

Fischer clearly provided an ''indication.'' That fact and his consistent use of Linnaean binomial nomenclature in the ''Elenchus'' demonstrate to us that the names Fischer provided for animals described by Azara (1801) are available. We thus consider Fischer's (1814) *megacephalus* to be the earliest valid name that can be applied to the *O.* ''*capito*'' complex.

Other researchers also regard Fischer's work to be available. His names are currently used for some muroid rodents (examples are *Calomys laucha* and *Reithrodon auritus* [see Musser and Carleton, 1993] and *Oxymycterus rufus* [recognized by Hershkovitz, 1994, in his review of the genus]) as well as other mammals that were originally described by Azara in 1801 (Langguth, 1966; Hershkovitz, 1987; Wilson and Reeder, 1993). In a list of the mammals described by Azara, Hershkovitz (1987: 62) used *megacephalus,* writing that it ''Antedates *Oryzomys capito* Olfers.'' More recently, ''*Oryzomys megacephalus*'' was used by Bonvicino et al. (1996) for one of the species encountered in a study of small mammals along the Rio Araguaia in central Brazil. And, in their list of the mammals of Provincia de Misiones, Chebez and Massoia (1996: 195) used the combination ''*Oryzomys megacephalus intermedius*'' for a species that had been identified as ''*Oryzomys capito intermedius*'' (see Massoia, 1974).

A neotype must be selected for *Mus megacephalus* Fischer (1814) and we do so in Taxonomic Summary. Six other names apply to this Amazonian species but were proposed after 1814: *capito* Olfers (1818: 209) and *cephalotes* Desmarest (1819: 63), both based on Azara's (1801: 82) ''Rat second, ou Rat à grosse tête''; *velutinus* Allen and Chapman (1893: 214); *goeldi* Thomas (1897: 494); *modestus* Allen (1899: 212); and *perenensis* Allen (1901: 406). Their identities and allocations are discussed in Taxonomic Summary.

Reinstating Fischer's *megacephalus* in place of Olfers' *capito* may seem to ''upset a long-accepted name in its accustomed meaning through the introduction of an unused name that is its senior synonym'' (article 23b in 1985 edition of the Code). Principle and concern for long-term nomenclatural stability, however, require the replacement of *capito* by *megacephalus.* Furthermore, although Olfers proposed *capito* in 1818, we emphasize that its availability was unrecognized until 1959 when Hershkovitz brought Olfers' names to the attention of systematists, and that it has been in general use only since 1961 with the publication of Cabrera's ''Catálogo de los mamíferos de América del Sur.'' Before then *capito* itself was virtually a ''forgotten name.'' Since 1961, *capito* has been used in the taxonomic and ecological literature of Neotropical muroids, but it was never defined or diagnosed and its ''accustomed meaning'' changed substantially. Hershkovitz (1960) and Cabrera (1961), for example, subsumed a plethora of scientific names under *Oryzomys capito,* but most of them are tied to holotypes representing different species. Whatever concept of *capito* existed in the 1960s was altered by Gardner and Patton in 1976 when particular names were removed from their place in the synonymy of *capito* and applied to other species. Gardner and Patton certainly provided the beginnings of a reasonable morphological and chromosomal diagnosis of *capito,* but the species remained undefined geographically and for other traits. Even after their report, the literature demonstrated different ''meanings'' of *capito* depending on the author. In the *Mammals of North America,* for example, Hall (1981) recognized the species in Central America, but later authors would identify that geographic segment as *O. talamancae* and demonstrate that *O. capito* did not occur west of the Andes in the trans-Andean region (Gardner, 1983a; Musser and Williams, 1985). Ignorance about the characteristics of *capito* continued even after 1985, as exemplified by the statement announcing *capito* to be ''extensively distributed in South America'' (Fonseca and Kierulff, 1988).

The ''accustomed meaning'' of *Oryzomys* ''*capito*'' might be modified even more drastically. If the presence of western and eastern

TABLE 3

Results of Principal Components Analyses of Adult *Oryzomys megacephalus* from Western (Amazonas, Rio Juruá, sample 28), Central (Pará, Itaituba-Jacaréacanga, sample 38), and Eastern (Mato Grosso, Serra do Roncador, sample 35), Exemplar Localities in the Amazon Basin of Brazil
(Samples used for the analyses are described in table 1, and specimens measured listed in appendix B. See fig. 12.)

	Principal components			
	Amazonas and Mato Grosso		Amazonas, Pará, and Mato Grosso	
Variable	First	Second	First	Second
ONL	0.069	−0.003	0.061	0.003
ZB	0.069	0.007	0.061	0.003
IB	0.050	0.022	0.043	0.006
LR	0.078	−0.001	0.070	−0.002
BR	0.071	0.010	0.072	−0.010
LB	0.062	0.003	0.053	0.007
HBC	0.053	0.003	0.047	0.005
BZP	0.091	0.008	0.081	0.015
LD	0.097	−0.009	0.086	0.004
LBP	0.103	0.022	0.085	0.030
PPL	0.063	−0.008	0.062	−0.006
LIF	0.061	−0.065	0.052	−0.038
BIF	0.038	−0.011	0.048	−0.062
CLM1–3	0.047	0.004	0.039	0.009
BM1	0.050	0.005	0.042	0.014
Eigenvalue	0.072	0.006	0.058	0.007
% Variance	75.4	6.1	68.3	8.2

Amazonian groups, which now appear to be defined by morphological as well as chromosomal and molecular traits, is substantiated by study of additional samples, and two species objectively defined, the application of scientific names would change. As a consequence, populations from the western portion of the Amazon Basin in Bolivia, Perú, Ecuador, Colombia, and western Brazil would represent one species, for which the oldest name is *perenensis* (Allen, 1901). Populations from the Guiana Region, Trinidad, eastern and southern Venezuela, central and eastern region of the Amazon Basin, and eastern Paraguay would constitute the other species, which would bear the name *O. megacephalus*. In this arrangement, the currently used *capito* would be severely restricted in population and geographic reference compared with its former scope, and the argument that it be retained for the sake of nomenclatural stability would be even less credible.

ORYZOMYS MEGACEPHALUS (Fischer, 1814)

Characterization of the Species

In our view, *Oryzomys megacephalus* is characterized by the geographic variation in cranial and dental dimensions, chromosomal traits, and sequence variation outlined previously. It is a species of medium body size with a tail slightly longer than head and body (table 4); its external appearance (fig. 7) was accurately characterized by Gardner and Patton (1976: 39):

> dorsal adult coloration usually buffy brown to yellowish brown (but rufous in some individuals), usually with a broad, darker, mid-dorsal stripe, and with gradation to paler and grayer laterally (immatures dark gray-brown dorsally); ears clothed externally with dark brown hairs and internally with a mixture of whitish and dark brown hairs . . .

To this description can be added front and hind feet covered by white hairs, claws partially concealed by long and silvery ungual hairs; elongate hind feet with the full complement of plantar pads (see fig. 17); superciliary, genal, and mystacial vibrissae extend to ears but not beyond their posterior margins, when appressed against stuffed skin; and four pairs of mammae (one pectoral, one postaxillary, one abdominal, and one inguinal).

Typical conformation of the cranium and mandible of *O. megacephalus*, no matter whether collected in the western or eastern portions of its range, is exemplified by the Peruvian and Paraguayan specimens illustrated in figures 8 and 9; molar occlusal surfaces are depicted in figure 10. The following combination of traits is distinctive: moderately long rostrum, smooth or only slightly raised lateral interorbital margins, short and broad incisive foramina shaped like a teardrop, long bony palate, no sphenofrontal foramen or squamosoalisphenoid groove, but stapedial foramen present (modified carotid arterial pattern similar to that diagramed for *Oligoryzomys* by Carleton and Musser, 1989; a pattern also shared by *O. yunganus*—see account of that species), each second upper

TABLE 4

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weights (g) from Selected Samples of *Oryzomys megacephalus* and *Oryzomys laticeps*

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. Each sample contains the range in age from young to old adults. Number preceding country refers to numbered sample in table 1 and appendix B, where, unless otherwise indicated in footnotes, specimens measured are identified.)

Sample	LHB	LT	LHF	LE	W
Oryzomys megacephalus					
1. FRENCH GUIANA[a]	127.1 ± 6.11 (116–139) 14	115.2 ± 7.53 (100–130) 14	28.3 ± 1.00 (27–31) 14	19.4 ± 0.63 (19–21) 14	—
3. GUYANA	124.0 ± 9.88 (107–139) 12	102.2 ± 13.13 (82–103) 12	27.8 ± 1.12 (26–30) 13	19.6 ± 1.04 (18–21) 13	51.9 ± 9.13 (37–67) 13
5. VENEZUELA	120.0 ± 9.89 (99–142) 32	116.2 ± 7.57 (90–132) 32	28.2 ± 1.35 (25–32) 32	—	—
15. PERÚ	129.7 ± 10.80 (112–148) 21	114.0 ± 7.08 (102–129) 17	30.8 ± 1.50 (29–35) 22	21.0 ± 1.60 (19–25) 13	74.2 ± 14.09 (59–90) 9
18. BOLIVIA[b]	135.8 ± 9.78 (114–155) 18	116.5 ± 6.62 (101–128) 18	30.7 ± 1.88 (29–33) 18	21.6 ± 1.66 (18–26) 17	—
23. BRAZIL	130.2 ± 8.35 (119–145) 21	121.7 ± 8.25 (106–133) 21	32.1 ± 0.85 (31–34) 21	20.5 ± 0.87 (18–22) 21	59.2 ± 12.56 (41–80) 21
28. BRAZIL	134.6 ± 8.33 (119–155) 30	126.5 ± 7.88 (109–145) 27	32.5 ± 1.38 (30–35) 30	20.9 ± 1.18 (18–23) 28	71.3 ± 11.99 (48–94) 27
37. BRAZIL	124.9 ± 11.22 (110–141) 10	116.6 ± 5.70 (109–127) 10	30.0 ± 0.82 (29–31) 10	20.6 ± 0.97 (19–22) 10	66.1 ± 12.86 (52.3–95.3) 10
43. PARAGUAY	134.5 ± 9.30 (113–146) 13	122.8 ± 7.83 (112–135) 13	30.9 ± 1.12 (29–33) 13	21.4 ± 1.39 (19–23) 13	63.8 ± 11.73 (49–86) 12
Oryzomys laticeps					
44. BRAZIL[c]	145.3 ± 9.71 (135–158) 6	142.8 ± 8.28 (131–152) 6	33.7 ± 1.21 (32–35) 6	23.3 ± 1.21 (22–25) 6	—
45. BRAZIL[d]	146.7 ± 3.22 (143–149) 3	128.3 ± 4.73 (123–132) 3	33.3 ± 0.56 (33–34) 3	21.7 ± 0.56 (21–22) 3	70.7 ± 3.06 (68–74) 3

[a] AMNH 266494, 266508, 266514, 266518, 266519, 266521, 266527, 266530, 266533, 266534, 266538, 266541, 267016, 267018.

[b] AMNH 209964, 209966, 209970, 209974, 209979, 209980, 209983, 209988, 209989, 209991, 210002, 210003, 210005, 210019–210021, 210361, 246149.

[c] BMNH 3.10.1.42 (holotype of *O. oniscus*), 3.10.1.43–3.10.1.47.

[d] USNM 304571, 545059, 545056.

molar with a long paraflexus and without a medial fossette (“enamel island lacking,” as described by Gardner and Patton, 1976: 39), each second lower molar nearly bisected by a deep hypoflexid (fig. 10), and diploid numbers of either 52 (table 13) or 54 (fig. 11; table 13). Taken together, these traits can be used to distinguish examples of *O. megacephalus* from specimens of *O. talamancae, O. bolivaris, O. yunganus, O. nitidus, O. macconnelli, O. russatus,* and the two new species described here (see summary fig. 151 and table 52).

GEOGRAPHIC DISTRIBUTION

Oryzomys megacephalus occurs primarily in tropical evergreen rainforest formations (which include riverine or gallery forest in the Brazilian Cerrado) in the Río Orinoco basin in southern Venezuela (also see Ochoa et al., 1993), the Guiana Region (including the

Fig. 7. *Oryzomys megacephalus* (MHNLS 8090), an adult male from 5.2 km NE San Ignacio de Yuruaní, 850 m, Estado de Bolívar, Venezuela, collected June 30, 1987. Prints were generously provided by R. S. Voss.

tepuis of eastern Venezuela), the island of Trinidad, and drainage basin of the Amazon River. The range, as estimated from specimens we have seen is, except for the eastern Paraguayan segment, primarily concordant with the definition of Amazonia (see map in fig. 15) and generally similar to that of *O. yunganus* (see map in fig. 14) and *O. macconnelli* (see map in fig. 78). The western limits of *O. megacephalus* are physiographically and ecologically defined by the eastern foothills of the Andes from Bolivia to Colombia. The northern limits are defined by the Llanos of the Orinoco in western and northern Venezuela and by the coastal dry zone of the Río Unare drainage between western and eastern coastal ranges of Venezuela (see map in fig. 66 and discussion of the range relative to that of *O. talamancae* in the account of that species). Our westernmost record in coastal Venezuela is from the upper Neverí Valley (10°03′N/64°38′W) at 732 m in the eastern coastal highlands south of Cumaná (see gazetteer for *O. megacephalus*, which follows the gazetteer for *O. talamancae*). We note that *O. megacephalus* is represented in the eastern coastal mountains of Venezuela by the series from Neverí and the holotype of *modestus* from Campo Alegre at 915 m (see discussion of *modestus* in Taxonomic Summary), but has yet to be recorded from the western coastal mountains, which are inhabited by *O. talamancae* (fig. 66).

The northern boundary of *O. megacephalus* ranges east of about longitude 65°W and coincides with limits of rainforest habitats along the coast from eastern Venezuela to the Belém region of northeastern Brazil, except for the population on Trinidad. The species apparently is absent from the semiarid caatinga. It either has not been collected there (Mares et al., 1981a, 1985; Streilein, 1982; Willig and Mares, 1989) or has been misidentified. We have no records of specimens east of about longitude 47°W. Samples of *O. megacephalus* have been recorded from gallery forests in the cerrado south of Brasília under the names ‘‘*capito*’’ (Alho et al., 1986; Mares et al., 1989), or ‘‘*oniscus*’’ (Alho, 1982). We have not seen those specimens reported by Alho et al. (1986) and Alho (1982), but we have studied half of the series documented by Mares et al. (1989) and all are examples of *O. megacephalus* (sample 37, table 1). We also have not seen the specimens of ‘‘*Oryzomys megacephalus*’’ reported by Bonvicino et al. (1996) from gallery forest and cerrado along the upper reaches of the Rio Araguaia in eastern Mato Grosso and western Goiás.

The southern distributional boundaries also need to be determined. Our most southern record is near Las Cruces in Bolivia (17°47′S/63°22′W). The species has not been reported from farther south in the Pantanal, of Mato Grosso do Sul (Alho et al., 1987) and we have not seen any material from the Chaco Boreal of Paraguay and southern Bolivia (see Myers and Wetzel, 1983, and references they cite for descriptions of the Paraguayan Chaco). In Paraguay, Myers (1982) collected samples of *O. megacephalus* from east of the Río Paraguay, but not from the Chaco Boreal west of the river.

GEOGRAPHIC VARIATION

Within *Oryzomys megacephalus*, geographic variation in morphometric traits is related to overall body size and forms a primary pattern consisting of basically western and eastern Amazonian clusters. However, we do not recognize each as a species, even though variations in sequence and chromosomal data reinforce the morphometric distinctions. Information about variations in biochemical and chromosomal traits is still meager; very few samples have been analyzed, and none from geographic regions between the two groups. The apparent concordance of the present scanty chromosomal and biochemical data with morphometric results needs to be tested by obtaining more samples from within the range of each cluster, and from unsampled areas between them—in central Amazonia between the Rio Juruá and the Itaituba region, for example.

Our morphometric analyses of cranial and dental data also require testing by additional samples from relevant geographic areas. We can separate most specimens currently available to us into an eastern or western Amazonian group based on simple qualitative inspection of the skull, as well as by multivariate statistical analyses. Some samples, how-

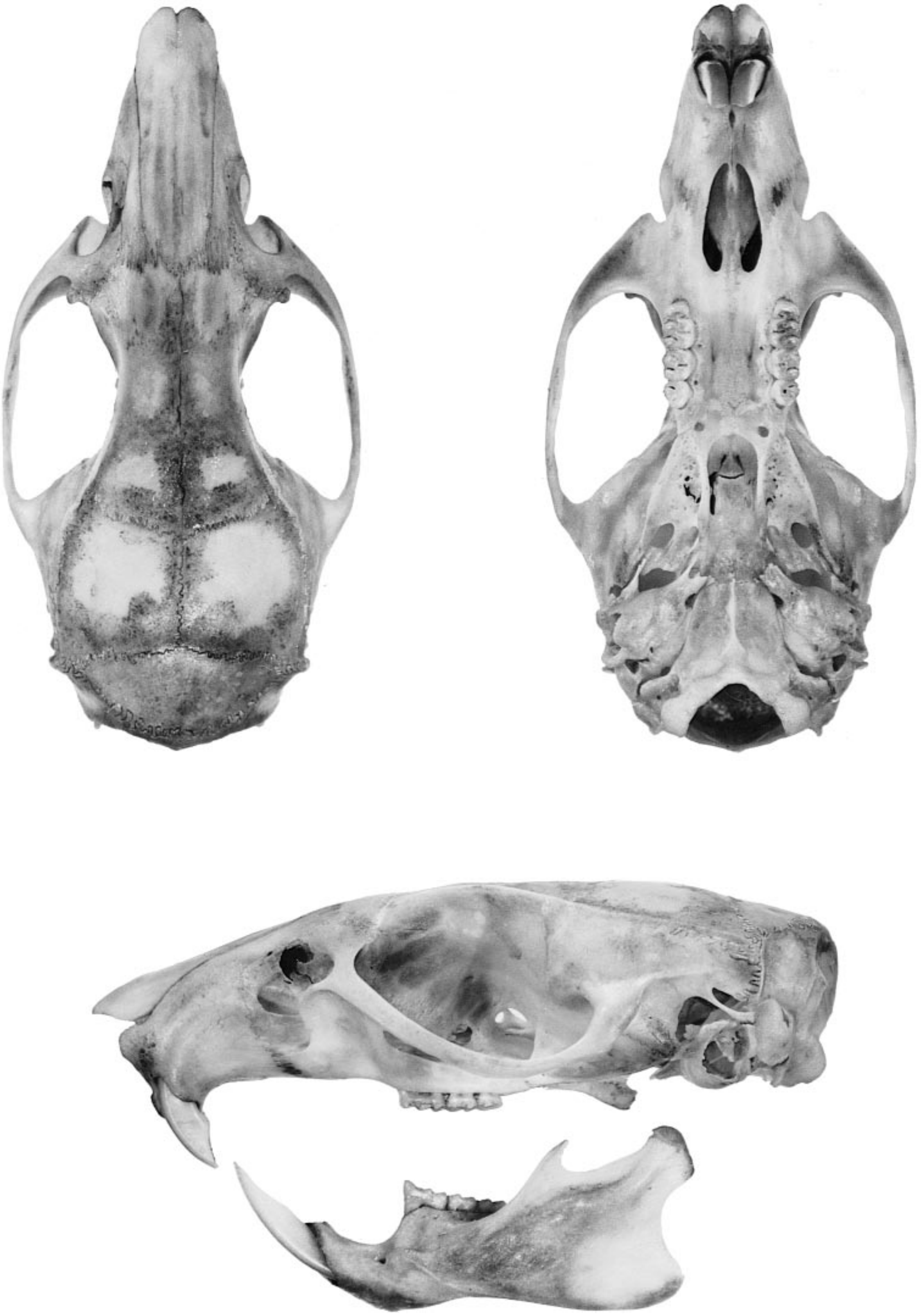

Fig. 8. Cranium and dentary of an example of large-bodied *O. megacephalus*, which occurs in the western Amazonian portion of its geographic range. This adult (AMNH 230975) is one of the measured specimens in sample 13 (table 1; appendix B) from San Pablo, Departamento de Pasco, Perú. ×3.

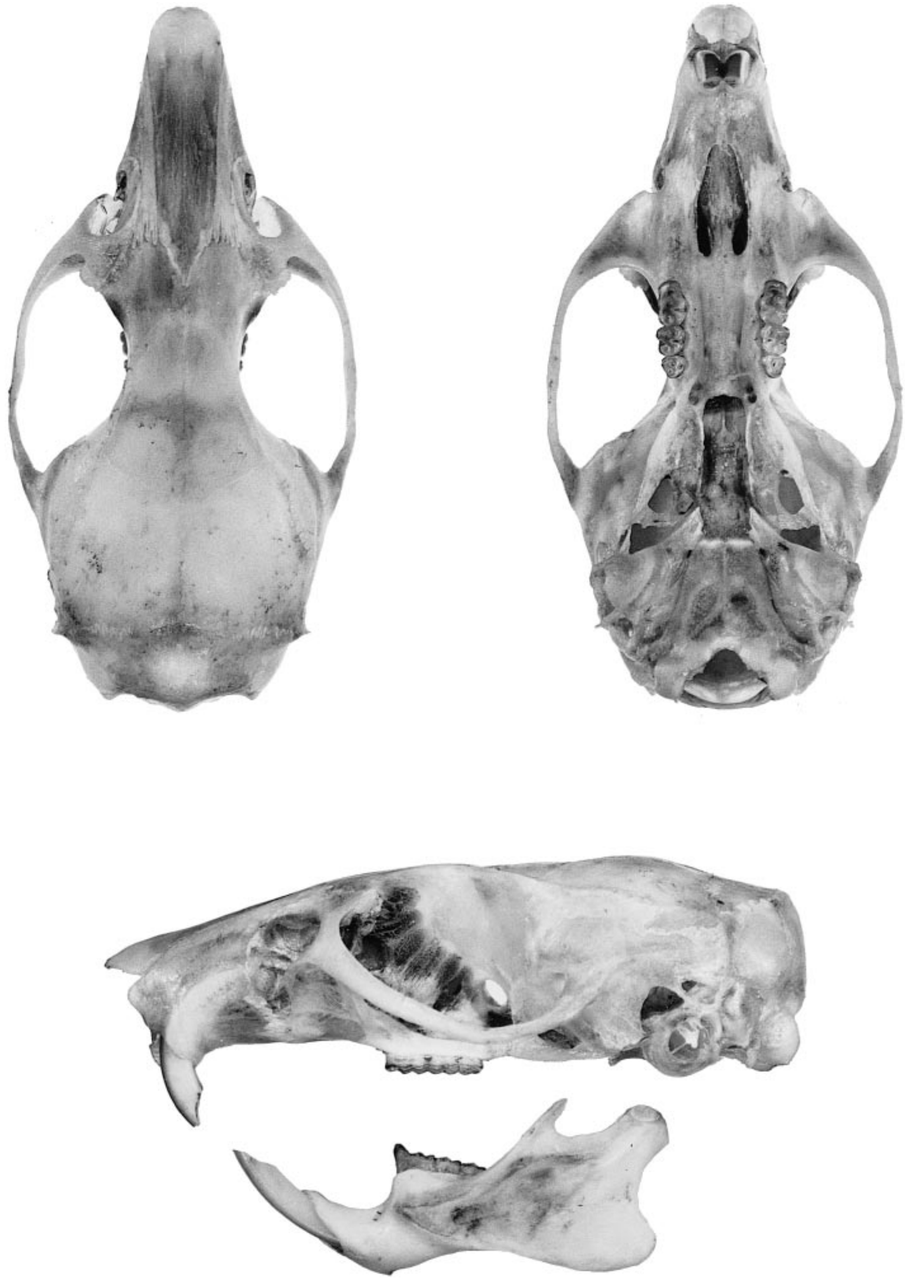

Fig. 9. Cranium and dentary of an example of the small-bodied *Oryzomys megacephalus*, which is found in the Guiana region, central and eastern Amazonia, and eastern Paraguay. This adult (USNM 549544) is from east bank of Rio Xingu, 52 km SSW Altamira, Estado de Pará, Brazil (03°39′S/52°22′W). ×3.

Fig. 10. Occlusal views of right upper (CLM1–3 = 5.0 mm) and lower (clm1–3 = 5.4 mm) molar rows from *Oryzomys megacephalus* (AMNH 231655) collected at Nevati Mission, Departamento de Pasco, Perú. The patterns formed by cusps and folds are characteristic of the species. Note also that a labial fossette (**lf**) is present in the second upper molar (but not a medial fossette), and the paraflexus (**p**) is long. The second lower molar does not have a fossettid, is nearly divided by a long hypoflexid (**h**), and the opposing entoflexid (**ef**) is just a crease on the lingual surface. See also figures 29–32.

ever, do not readily fit within this picture; two in particular illustrate the difficulty of assigning specimens to one or the other clusters. One of these consists of 10 specimens from the Federal District in Brazil south of Brasilia (sample 37, table 1). Geographically, this sample should fall within the group characterized by small skulls, yet it joins the western Amazonian assemblage in the cluster (fig. 4) and principal components analyses (fig. 5, diamond). Compared to the other samples from the eastern margins of the Amazon Basin (including another sample from nearby Goiás, 36 in table 1 and fig. 5), the series from near Brasilia averages larger in cranial and dental dimensions. We suspect this may just be a reflection of the real range of size variation within the eastern Amazonian group because other specimens from the same reserve south of Brasilia have been shown to have a diploid number of 54 (table 13), which seems to be common to the small-bodied form. However, larger series from the Federal District need to be obtained and analyzed to really understand the significance of the variation we record in the small sample available to us.

The other sample (38 in table 1, Pará-1 in fig. 4, and fig. 5) comes from about 200 km south of Itaituba from along the western side of the Rio Tapajós in west-central Pará. This sample clusters with the small-bodied eastern Amazonian segment and is close to samples from southern Venezuela and eastern Paraguay (fig. 4). The actual range in size among the adults of comparable age, however, extends from large skulls, typical of those characterizing samples from western Amazonia, to smaller skulls, which closely resemble those specimens from most samples in eastern Amazonia. Results of principal components analyses of Brazilian samples illustrate the problem (fig. 12). In the upper diagram of figure 12, we contrast two geographical extremes in the Amazon Basin: a western sample from the Rio Juruá in western Amazonas (longitude 70°45′W), and an eastern series from Serra do Roncador in Mato Grosso (longitude 51°46′W). In the lower diagram, we retain the same samples but add sample 38 from along the western (left) side of the Rio Tapajós (longitude 56°–58°W). The distribution of specimen scores along the first axis in the upper graph indicates only slight overlap between the samples from the Rio Juruá in the west and Serra do Roncador to the east. In the lower graph, specimens from about 200 km south of Itaituba along the western side of the Rio Tapajós overlap scores representing both the eastern and western samples. The dispersion of specimen scores along the first principal component in each graph is influenced by nearly all cranial

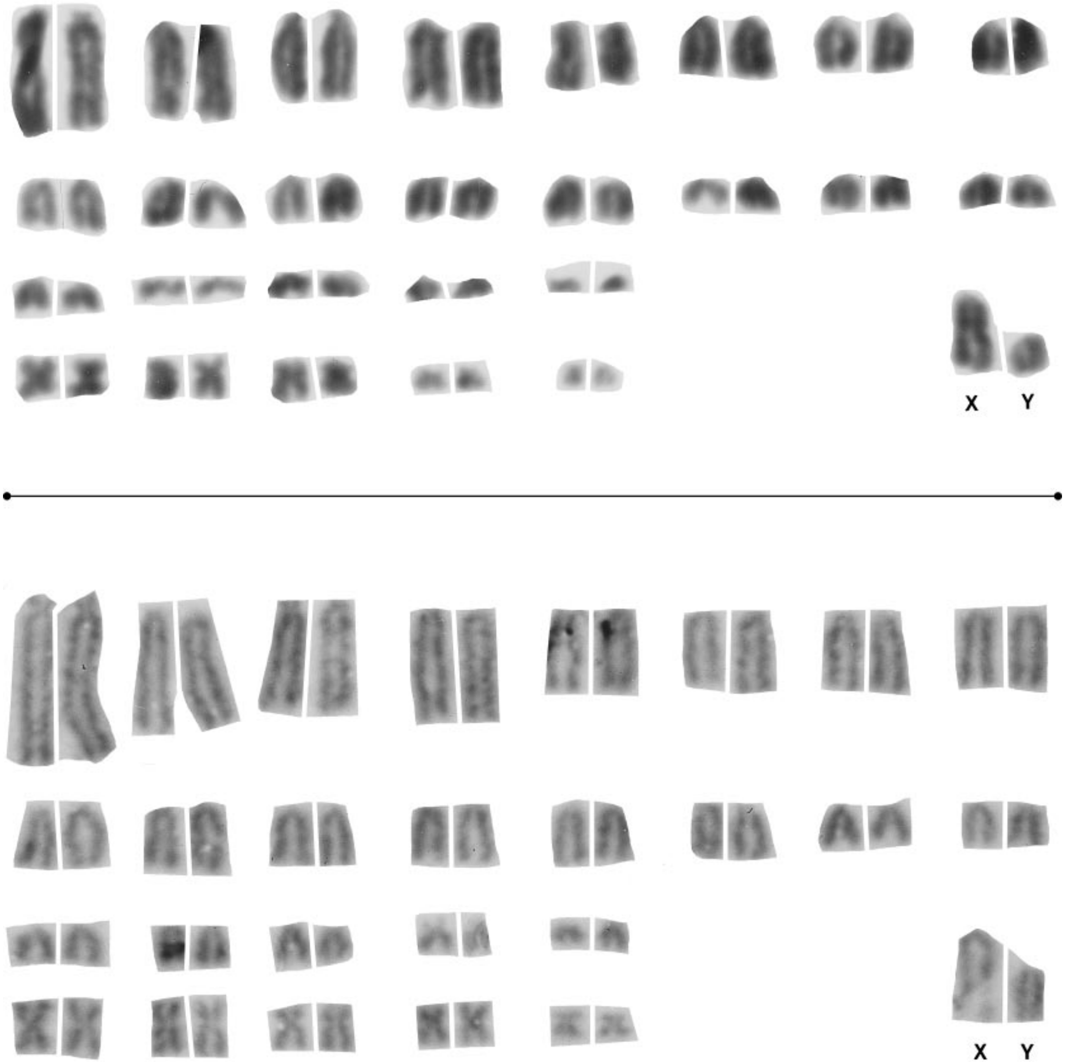

Fig. 11. Karyotypes from male *Oryzomys megacephalus* (2*n* = 54, FN = 62) from the eastern portion of its geographic distribution. **Top**: Neotype (UMMZ 133811) from eastern Paraguay, Departamento de Canendiyu, 13.3 km N Curuguaty (24°31′S/55°41′W). **Bottom:** USNM 549549 from Brazil, Estado de Pará, east bank of Rio Xingu, 52 km SSW Altamira (03°39′S/52°22′W).

Autosomes consist of 5 pairs of medium-sized to small metacentrics and submetacentrics and 21 pairs of telocentrics of which the first is very large and the remaining 20 pairs grade from large to small. The first and third largest telocentrics bear short second arms. A large telocentric X and smaller telocentric Y form the sex chromosomes. This complement is common to samples documented from the eastern portion of the range of *O. megacephalus* representing populations of small-bodied animals. The larger bodied populations sampled from western Amazonia are characterized by 2*n* = 52 and FN = 62 (see table 13 and discussion in text).

and dental measurements (table 3), reinforcing the perception derived from qualitatively inspecting the skulls that populations in the western Amazon Basin of Brazil are characterized by animals of significantly larger body size than are those in eastern Brazil at the latitude of eastern Mato Grosso. These extremes, however, seem to be connected by

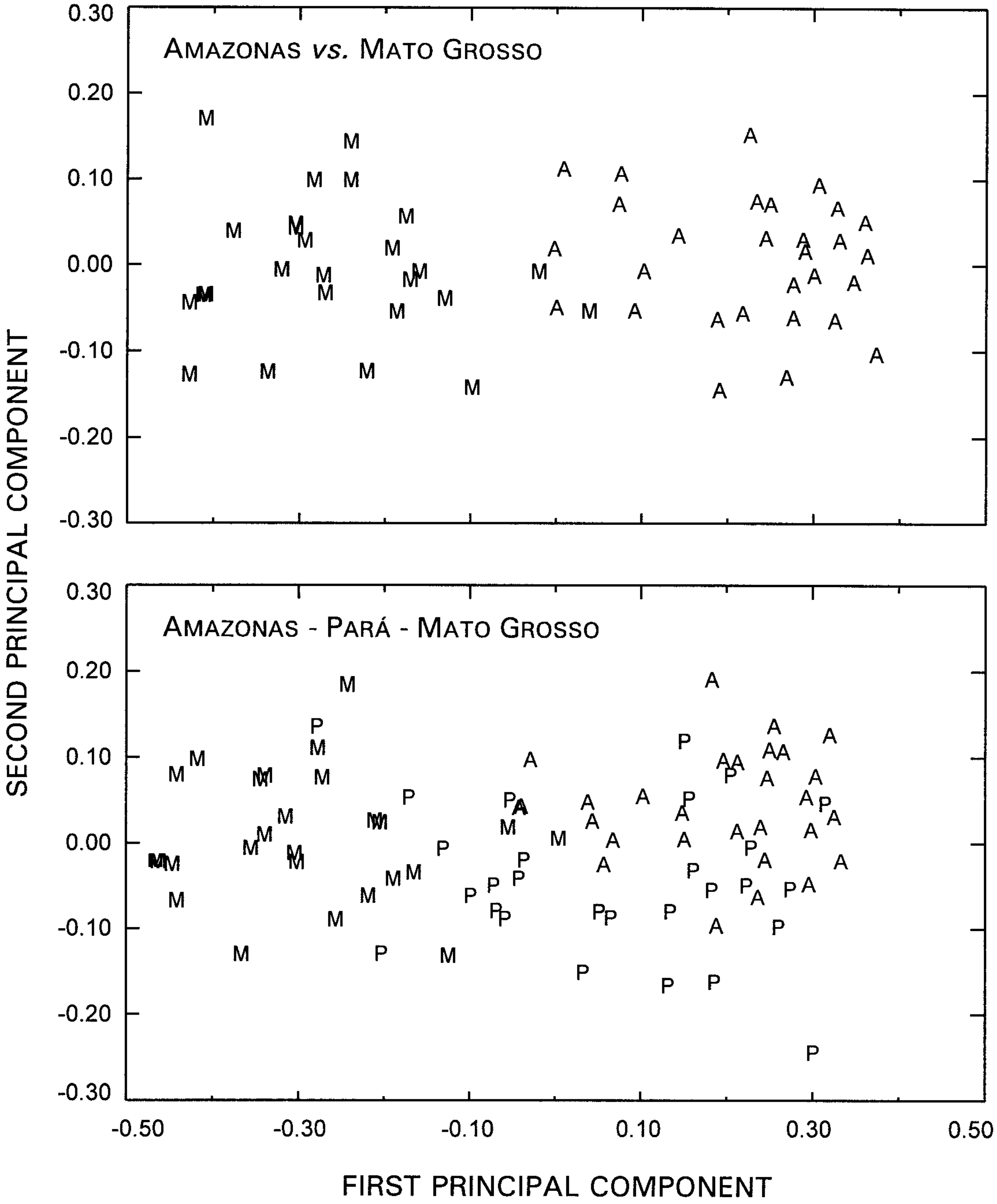

Fig. 12. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 3) and projected onto the first and second principal components extracted from analysis of young to old adult *Oryzomys megacephalus* in three samples representing far western, central, and far eastern longitudes in the Amazon Basin of Brazil. **Upper diagram:** Western sample from Penedo, along the Rio Juruá, in western Amazonas, longitude 70°45′W (**A**; sample 28 in table 1; *N* = 29) contrasted with an eastern sample from Serra do Roncador in eastern Mato Grosso, longitude 51°46′W (**M**; sample 35 in table 1; *N* = 26). **Lower diagram:** The western and eastern samples from Penedo and Serra do Roncador, respectively, compared with a sample from central portion of Amazon Basin between Itaituba and Jacaréacanga along the Rio Tapajós in western Pará, Brazil, longitude 56°–58°W (**P**; sample 38 in table 1; *N* = 29). See discussion in text.

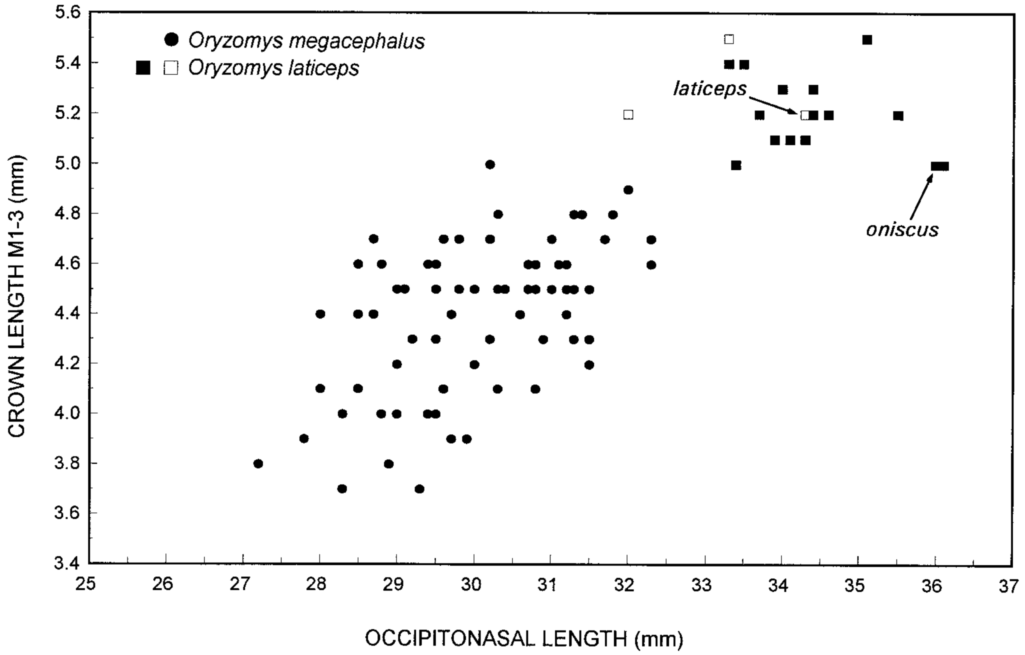

Fig. 13. Discrimination between *Oryzomys megacephalus* and *O. laticeps* from Brazil by lengths of cranium and molar row. Specimens of *O. megacephalus* (*N* = 73) represent the populations characterized by small cranial dimensions from the eastern rim of the Amazon Basin in eastern Pará (sample 41 in table 1), Goiás (sample 36), and Mato Grosso (sample 35). The 18 examples of *O. laticeps* come from the Atlantic region in the Brazilian states of Pernambuco, Bahia, Espírito Santo (■: BMNH 3.10.1.42, 3.10.1.43, 3.10.1.45, 3.10.1.46, 3.10.1.48; KU 39316, 39352, 39354; LACM 62903, 62904, 62906; USNM 304571, 545055, 545056; UZM 1264), and Lagoa Santa in Estado de Minas Gerais (□: UZM 266, 269, 389; table 5). Squares representing the holotype of *oniscus* and lectotype of *laticeps* are indicated. See text for further discussion.

variation in the available samples from the intermediate longitude.

We studied the 29 specimens from along the Rio Tapajós to determine if both forms were possibly present in the sample. Primary variation in size is influenced by age—adults are larger (indexed by occipitonasal length) than young adults. However, among the adults are a few skulls that are obviously smaller than most of the other skulls of comparable age (judged by molar wear). An exemplar pair consists of the larger USNM 461943 (ONL = 34.2 mm, CLM1–3 = 4.6 mm) and the smaller USNM 545256 (ONL = 31.5, CLM1–3 = 4.5 mm); by using cranial size (but not toothrow length), the former could easily be identified as a member of the western Amazonian cluster, whereas the latter fits nicely into the eastern Amazonian group. Is the larger example a different species than the smaller, or are both simply part of the typical range in variation expected in samples from the region, or does sample 38 really represent morphological overlap between western and eastern segments and some degree of gene flow between them?

We do not know. The sample from the Rio Tapajós is the only one we have that is closest to our nearest western sample, which comes from along the Rio Juruá in western Amazonas. No biochemical or chromosomal data are available for it. Significance of the variation we recorded needs to be determined by acquisition and analyses of samples from the region between the Juruá and Tapajós rivers, and by collecting fresh samples along both banks of the Tapajós for analyzing biochemical and chromosomal variation. That action should be part of a larger effort to test our hypothesis that the intersample variation presented here actually represents a single species (*O. megacephalus*) by analyses of geographic variation in morphometric, biochemical, and chromosomal data from a larger number of samples gathered from throughout the range of *O. megacephalus*, particularly from surveys along certain transects.

The Rio Juruá could be used for a starting point in appropriate surveys. Specimens of *O. megacephalus* from along that river are clearly examples of the western group characterized by large body size (figs. 4, 5, 12), 2*n* of 52, and clustered closely by sequence data (fig. 6). Furthermore, gene flow estimates suggest ''there is no evidence of isolation by distance'' for *O.* ''*capito*'' (Patton et al., 1996: 234) either along the Rio Juruá (see fig. 43) or across the river (see figs. 41, 42) in the Headwaters, Upper Central, or Lower Central regions (sampling areas defined by Patton et al., 1994). Sampling along a transect beginning at some point on the right bank of the Rio Juruá and extending east to eastern Pará or southeast to Goiás and southeastern Mato Grosso would produce specimens from critical areas between documented localities containing the large animals to the west and the smaller rats to the east that could be used to test the integrity of our hypothesis (especially in the region along the Rio Tapajós between Itaituba and Jacaréacanga and along the opposite bank) as well as Patton's suggestion that the line between the two kinds of ''*capito*'' as defined by sequence variation lies along the ''Rio Madeira-Rio Negro axis, or east of there.'' Two other important transects could begin on the banks of the Amazon River opposite the mouth of the Rio Juruá. One survey could be made along a line north from the Rio Juruá through the Amazonas region of southern Venezuela and finish in the northeastern part of that state, or northeast through northwestern Brazil into the Guiana Region. The other survey should extend from the Rio Juruá east through the Manaus area into Amapá of northeastern Brazil. The line between the mouth of the Rio Juruá and the Manaus region is especially critical to understanding the variation in morphology, chromosomes, and sequence data over distance. In morphology, for example, our small series from near Manaus (sample 34; table 1, fig. 5) is somewhat intermediate in dimensions between samples from the western and eastern portions of the Amazon Basin (fig. 5) but has a diploid number of 54, which is characteristic of the small-bodied eastern group of *O. megacephalus* (table 13).

We note that geographic boundaries of western and eastern segments of *O. megacephalus,* as delimited by morphometric, chromosomal, and molecular traits, roughly correspond to geographic distributions of two groups of echimyid rodents in the genus *Proechimys* (*P. simonsi* and *P. guyannensis*), as mapped and discussed by Patton (1987). For him, the ''*simonsi*-group is geographically restricted to the western margins of the Amazon Basin from northern Bolivia through eastern Perú and Ecuador to southeastern Colombia'' (p. 309), and the ''*guyannensis*-group'' is ''confined in its distribution to the Guianan region and southern Venezuela through the central Amazon Basin of Brazil, with an isolate . . . in Minas Gerais and Goiás states in Brazil'' (p. 308). Patton also noted (p. 338) that the ''*guyannensis*-group members are close to *P. simonsi* [he regards the ''*simonsi*-group'' as a single species] in most salient features.'' Differences do exist in dental patterns, ''but these could represent nothing more than geographic variation. Only the analysis of samples from the hiatus in western Brazil between the known distributions of these taxa . . . will permit such a determination. . . . Future work may indicate that these groups should be condensed into one.'' (p. 338). Results of recent surveys have extended the range of *P. simonsi* in western Brazil to the Rio Urucu, southeast of Tefé on south side of the Rio Solimões (da Silva, 1995); the geographic distribution is now nearly concordant with that of the western segment of *Oryzomys megacephalus.*

ORYZOMYS LATICEPS (Lund, 1840)

CHARACTERIZATION AND COMPARISONS

This name covers the series from the Brazilian states of Pernambuco, Bahia, and Espírito Santo (44–46; table 1), localities in the Atlantic coastal rain forests (see the summarized range of rainforest formations on the

TABLE 5
Selected Measurements (mm) of Four Adult *Oryzomys laticeps* from Lagoa Santa in the Brazilian State of Minas Gerais[a]

	Lectotype UZM 266	UZM 268	UZM 269	UZM 389
ONL	34.3	—	33.3	32.0
ZB	17.7	17.0	—	16.7
IB	5.4	5.5	5.2	5.1
BR	7.0	6.5	7.1	6.3
LB	—	13.1	12.6	12.2
BZP	3.8	3.5	3.6	3.4
LBP	7.1	6.9	7.0	7.1
CLM1–3	5.2	5.2	5.5	5.2

[a] A. L. Gardner measured these specimens at the Universitets Zoologisk Museum in Copenhagen in 1978. At that time, he was taking measurements that did not include some of those employed for this report, so we lack a complete set of data for the Copenhagen material. See text for description of lectotype and information about the other specimens.

map in Hueck and Seibert, 1981, and in Prance, 1989: 105). These samples contain animals of large body size. Mean values of their cranial and dental dimensions cluster them with samples from western Amazonia, not with those from the adjacent eastern Amazonia and eastern Paraguay (figs. 4, 5). The available chromosomal data also indicate that the two groups share a 2*n* of 52; however, molecular evidence (mtDNA sequence data) separate the Atlantic rainforest samples from both the western and eastern Amazonian segments of *O. megacephalus* (fig. 6).

To the analytic samples from the Atlantic region (table 1), we also add four specimens (table 5) that critically bear on the nomenclature of *O. laticeps.* All were collected, presumably in forest (see Christiansen and Pitter, 1997, for a brief description of the original vegetation), at Lagoa Santa (19°38′S/43°53′W) in Minas Gerais. That locality is in the valley of the Rio das Velhas (Voss and Myers, 1991: 415), one of the tributaries of the Rio São Francisco, which flows north in northeastern Brazil to eventually empty into the Atlantic. Of the four, one is the lectotype of *O. laticeps* (a designation we document in Taxonomic Summary), which was described by Lund in 1840 and is the oldest name available for populations of the *Oryzomys* "*capito*" complex in eastern Brazil. Synonyms of *O. laticeps* are *Calomys saltator* Winge (1887) and *Oryzomys oniscus* Thomas (1904), allocations that are explained in Taxonomic Summary.

Samples of *O. megacephalus* closest to the distribution of *O. laticeps* are from regions to the west of coastal Brazil in rain forests of northeastern Pará (samples 41–43, table 1), and gallery forests in the cerrado of southeastern Mato Grosso (sample 35; table 1) and east-central Goiás (Anápolis, sample 36; table 1), localities that are all within the drainage basin of the Amazon River.

The robust size of specimens from the Atlantic rain forests and Lagoa Santa, in contrast to those from farther west in Pará and Mato Grosso, is illustrated by the relationship between occipitonasal length and length of maxillary molar row shown in figure 13. Values for *O. megacephalus* are derived from specimens collected at the Serra do Roncador in Mato Grosso (sample 35; appendix B), Anápolis in Goiás (sample 36; appendix B), and examples from Pará near the rios Xingu and Tocantins and the Capim region (sample 41). The upper righthand plots are represented by the specimens from Pernambuco, Bahia, Espírito Santo, and Minas Gerais. This distribution of body size into eastern Amazonia and Atlantic Forest segments seems to be coupled with chromosomal and molecular discontinuities as well (judged from available samples) and suggests that each set of samples represents a different gene pool (see the preceding discussion in Analytic Samples and Variation Patterns). As a working hypothesis, we regard the samples from Pernambuco, Bahia, Espírito Santo, and Minas Gerais to represent a separate species, *O. laticeps.*

Our interpretation can be tested by analyzing the individual and geographic variation in larger samples collected along three transects. One survey should extend from north to south along the coastal and inland extent of Atlantic tropical and subtropical rainforest habitats in Brazil. Another should extend from the coastal rain forest that is the habitat of *O. laticeps* west across the Rio São Francisco into the riverine habitats in the cerrado of eastern Mato Grosso and Goiás where the smaller bodied *O. megacephalus* has been collected. Finally, because moist forests are essentially continuous between the Atlantic coast of southern Brazil and eastern Paraguay, the third transect should begin in eastern Paraguay, where *O. megacephalus* occurs, and extend eastward across the Rio Paraná into the subtropical forests of southern Brazil.

GEOGRAPHIC DISTRIBUTION

Oryzomys laticeps, like *O. megacephalus,* also inhabits lowland tropical evergreen rain forests. Judging from specimens we studied, *O. laticeps* occurs in the tropical and subtropical Atlantic rain forests of Brazil from Pernambuco south to Minas Gerais, but the actual range is likely more extensive. Svartman and Almeida (1992), for example, reported chromosomal data from a sample identified as *O. capito* (documented by Zanchin in a Master's thesis; see table 13) collected in the state of Paraíba, north of Pernambuco; judged by chromosomal traits, these are *O. laticeps.* Moojen (1952: 47) reported both *O. laticeps* (''oeste de Minas Gerais, Goiaz, Mato Groso'') and *O. oniscus* (''desde Pernambuco até o sul da Bahia) from Brazil. The samples reported as ''*Oryzomys capito*'' by Fonseca and Kierulff (1988) as well as by Stallings (1988), who surveyed in the Atlantic Forest of Minas Gerais at the Rio Doce State Park, may be *O. laticeps.* The most southern collection locality so far recorded may be that documented by Olmos (1991), who obtained specimens he identified as ''*Oryzomys laticeps*'' from the Atlantic Forest on the Serra de Paranapiacaba, southern São Paulo. Islands off coasts of the states of Rio de Janeiro and São Paulo have been surveyed for mammals but no *Oryzomys laticeps* were encountered (Fernandez et al., 1988; Olmos, 1996). Although northern and southern distributional limits are unknown, they may coincide with boundaries of the Atlantic rainforest formations in Brazil. In the early 1800s, the northern limit of the rain forest ''was at the level of Cape São Roque at 5°, in the state of Rio Grande do Norte,'' but ''Presently the northernmost reasonably certain primary forest is found more than 1000 km to the south, in the southern part of the state of Bahia'' (Por, 1992: 7 and map on p. 8). The southern limit, Por noted, ''is probably still the natural one and is situated at 30° S along river Taquari in the north of the state Rio Grande do Sul.'' *Delomys dorsalis,* another Atlantic Forest endemic, occurs as far south as Taquara in the state of Rio Grande do Sul (Voss, 1993), which is close to the southern margins of tropical and subtropical Atlantic Forest habitats; *O. laticeps* may also extend this far south. Western boundaries have yet to be resolved. The species has not been recorded from caatinga habitats west of the Atlantic Forest formations (Streilein, 1982; Willig and Mares, 1989). The specimens from Lagoa Santa constitute the farthest inland record that we can identify as *O. laticeps.*[2] That region is within what Hueck and Seibert (1981) identified as cerrado and riverine forest formations. Christiansen and Pitter (1997: 23) also noted that

> Lagoa Santa is situated in the contact zone between the once-continuous Atlantic forest to the east and the cerrado (savanna) region to the west. . . . The original vegetation in this contact zone was a mosaic of forest, cerrado and grassland. The tropical mesophytic, broadleaved forests (from evergreen to deciduous) in the area of Lagoa Santa . . . differ from the wet Atlantic forest in being drier, and having a shorter stature, a less diverse botanical composition, and fewer epiphytes. . . . Strips of forest extended into the area as a network along the rivers and as scattered patches on and around limestone outcrops. . . .

SUMMARY

Analyses of variation in cranial and dental measurements gathered from 48 samples of the *O.* ''*capito*'' complex suggest that at least

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[2] There is much to learn about the geographic distribution of *Oryzomys laticeps*. James L. Patton wrote us that he and his students have trapped ''in good forested regions in São Paulo state (Boraceia and Intervales),'' but did not obtain *O. laticeps*; instead, they found only examples of *O. intermedius* [= *russatus*] and *O. ratticeps* [= *angouya*]. Other Brazilian students of Patton surveyed small mammals in the Atlantic forests of Minas Gerais and Rio de Janeiro for Biodiversitas and collected *O. laticeps* only at sites located to the east of the longitude of Belo Horizonte (19°55′S/43°56′W; Paynter and Traylor, 1991: 70) in Estado do Minas Gerais, not in places to the west (Patton, personal commun.; letter in AMNH Mammalogy Archives). Lagoa Santa, the type locality of *O. laticeps*, lies slightly to the east and north of Belo Horizonte.

two species are present. *Oryzomys megacephalus* occurs in Amazonia (the Amazon Basin, Guiana Region), eastern Paraguay, and on Trinidad. Within *O. megacephalus,* patterns of morphometric variation disclose two population moieties, one in western Amazonia, the other in central and eastern Amazonia as well as eastern Paraguay. Limited data from chromosomal and molecular sampling reinforces results from morphometric analyses. However, the evolutionary interrelationship of these two groups—whether they represent separate gene pools, for example—has yet to be investigated. *Oryzomys laticeps* is found along the Atlantic Forest region of Brazil. No evidence exists to suggest that its populations along eastern and southeastern Brazil are genetically closely linked to those of *O. megacephalus* in eastern Amazonia.

Our analysis of samples of *O. megacephalus* and *O. laticeps* is the first to document broad geographic variation in size and shape of cranial and dental features over their respective ranges. Although the results are preliminary, we have been able to generate testable hypotheses regarding the significance of the geographic patterns revealed, and our documentation presents a refined level of resolution that can now be clarified by future inquiry drawing on more samples from critical geographic regions. Such results would answer questions about the occurrence of phenotypic and genetic variation and its significance to population differentiation in Amazonia and eastern Brazil. If future work substantiates our suspicion that *O. megacephalus,* as we have defined the taxon here, actually comprises two species, the name *perenensis* is available for the western Amazonia form. *Oryzomys megacephalus* would continue to be the correct name for the $2n = 54$ taxon whose distribution extends from Trinidad and the Guiana Region south through parts of Brazil to eastern Paraguay. For the purposes of our present report, readers can now understand our morphological and geographic definition of *O. megacephalus* when we contrast its characteristics with other oryzomyine species in the accounts that follow.

THE *ORYZOMYS YUNGANUS* GROUP: *O. YUNGANUS* AND A NEW SPECIES FROM ECUADOR, BOTH INDIGENOUS TO AMAZONIA

The taxon *yunganus* is one of those that Tate (1939: 190) grouped with *Oryzomys laticeps* and Cabrera (1961: 387) listed as a subspecies of *O. capito.* It was, however, originally described by Thomas (1902: 130) as a species and diagnosed by him as a ‘‘member of the *O. laticeps* group, most closely allied to *O. perenensis,* All., but more uniformly rufous.’’ Thomas’s description is accurate:

> Size about as in other members of the group. Fur close and glossy, about 9 millim. long on the back. General colour dark fulvous, finely and profusely lined with black. Head greyer, sides and rump clearer and stronger rufous. Under surface soiled whitish, the bases of the hairs slaty, their tips dull white; line of demarcation on sides fairly marked. Tip of muzzle whitish, base of whiskers brown, continuous with a dark ring round eyes. Forehead greyish, lined with black. Ears very short-haired, pale brown, not contrasting with the general colour. Hands and feet silvery white above. Tail almost naked, very finely scaled, whitish below proximally, the remainder greyish brown. Skull as compared with that of *O. perenensis,* shorter, with more expanded zygomata (in the aged type). Interorbital region narrower. Molars shorter, but much worn in the type.

Thomas summarized the account by noting that *yunganus* ‘‘may be distinguished from its other Andean allies by its more fulvous general colour, shorter molars, and narrower interorbital region.’’ (p. 130). He concluded with this reservation: ‘‘I confess that I think the various local forms of this intricate and difficult group might be more properly considered as subspecies than species; but as Dr. Allen has described the other forms as species, it will be less confusing to do the same in the present case.’’ (p.130). Thomas based his description on a single old adult collected from Charuplaya in Departamento de Cochabamba, Bolivia.

The form Thomas referred to as *O. perenensis* was named and diagnosed by Allen in

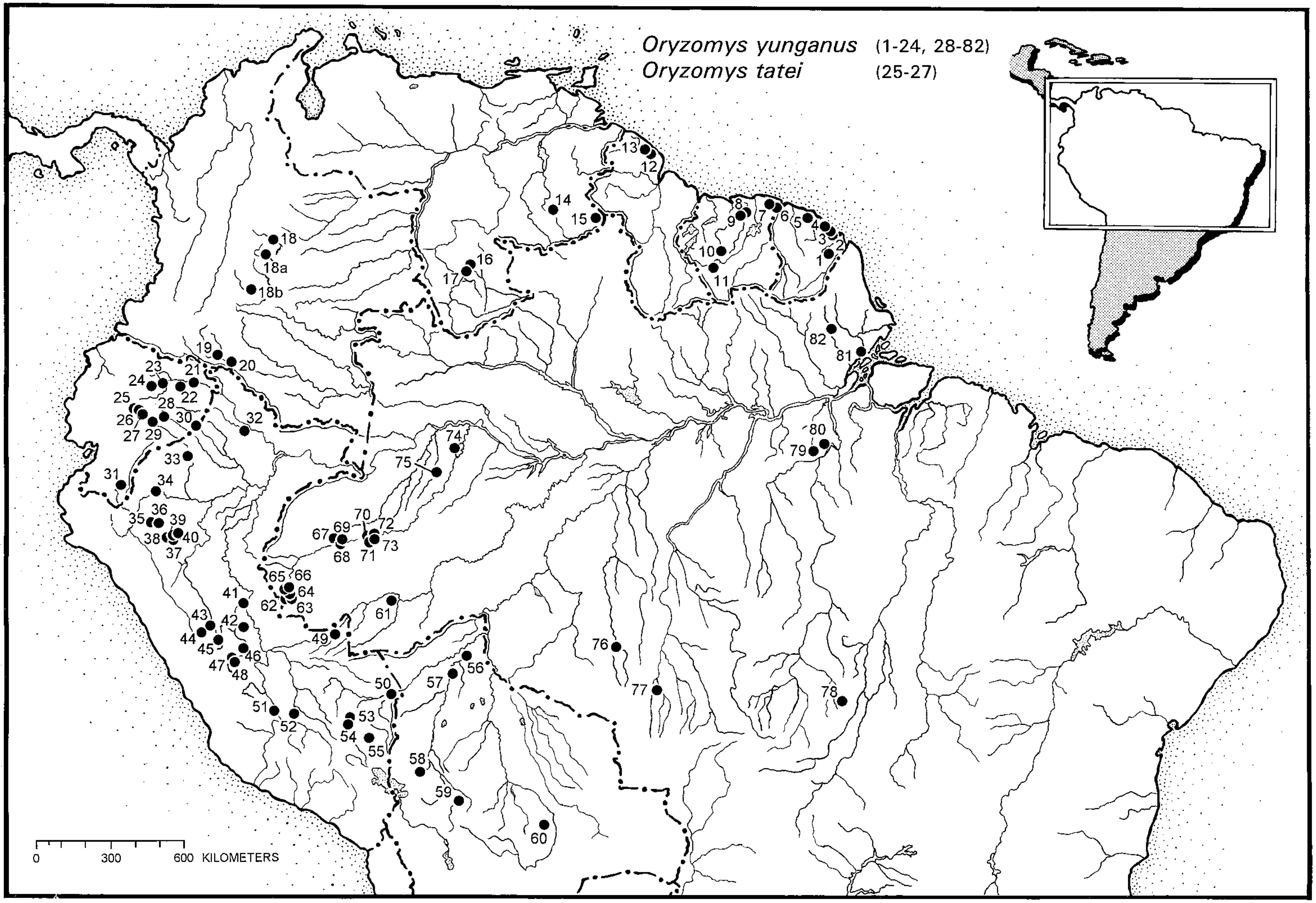

Fig. 14. Distribution of members of the *Oryzomys yunganus* group based on collection localities for the 476 specimens examined. Numbers index localities described in gazetteer for the group.

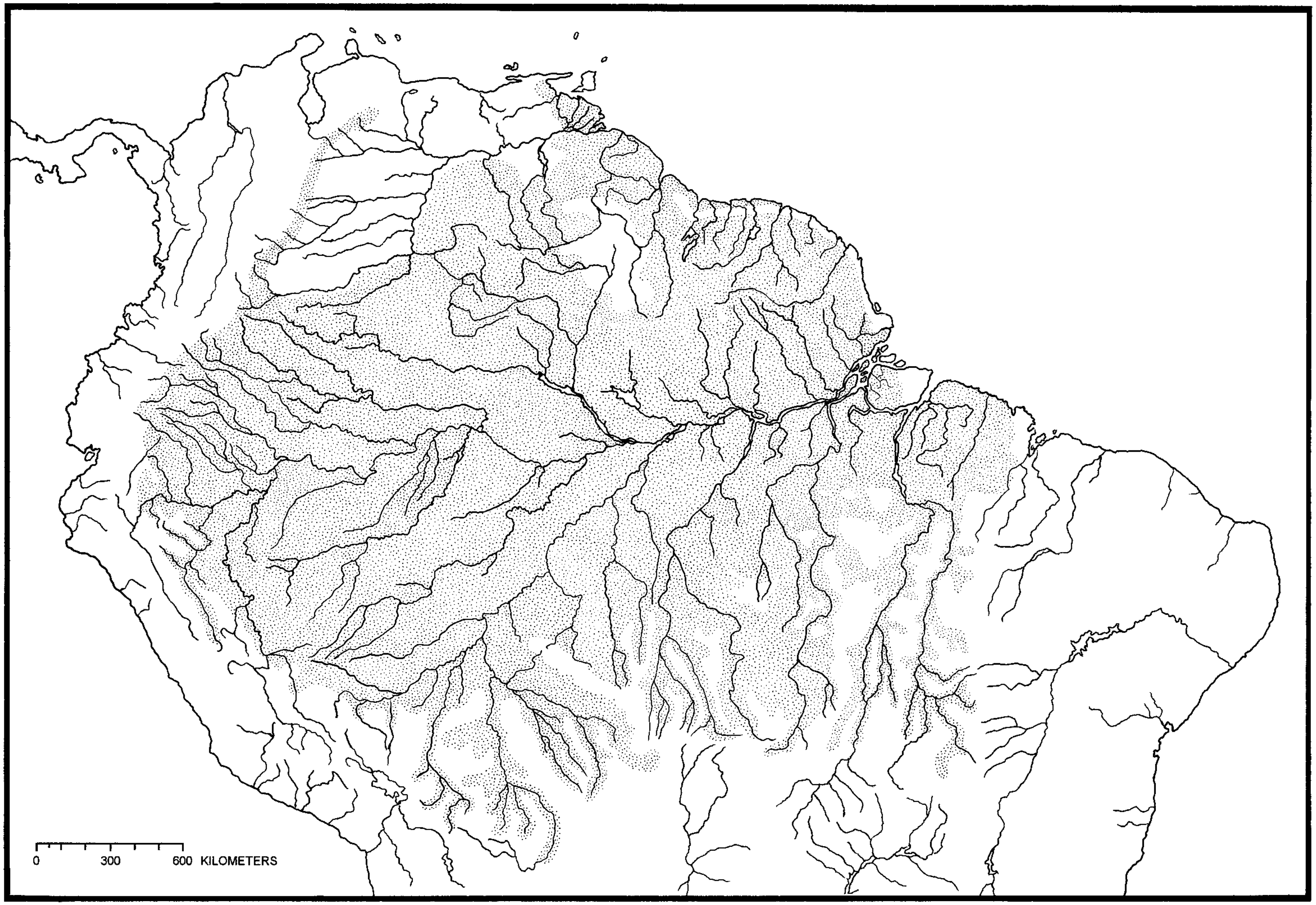

Fig. 15. Amazonia: The extent of lowland tropical evergreen rain forest in the Amazon Basin, southern and eastern drainage of the Río Orinoco, and the Guiana region. The map is based primarily on information in Hueck and Seibert (1981) as well as Voss (1991).

1901 (p. 406). It was a species, according to Allen, ‘‘very similar in coloration, texture of pelage, size and proportions to *O. magdalenae* Allen, but with the skull much broader and the dentition much heavier.’’ The holotype of *perenensis* (BMNH 0.7.7.25) was collected at Perené, 800 m (10°58′S/ 75°13′W), in Departamento de Junín, Perú. To us, that holotype has all the characters that we have come to associate with *O. megacephalus,* the species that in pelage coloration and general external and cranial morphology is most like *O. yunganus.*

Thirty years after Thomas's description was published, Gyldenstolpe (1932) arranged *perenensis* as a subspecies of *Oryzomys laticeps.* He listed *yunganus* as a species that was, borrowing phrases from Thomas, ‘‘most closely allied to *O. l. perenensis,* but more uniformly rufous. General colouration above dark fulvous, finely and profusely lined with black. Skull with narrower interorbital region and shorter toothrow.’’ (p. 18).

Thomas's *yunganus* retained its specific status during the next decade, as demonstrated by its listing in Ellerman's (1941: 354) monumental *Families and Genera of Living Rodents.* But by the 1960s, it was arranged as a subspecies of *O. capito* by Cabrera (1961: 387), and the identity of *yunganus* remained lost within the morass of names and characteristics associated with *O. capito* until 1976 when Gardner and Patton extracted it (p. 40):

> Another species we have distinguished within the ‘‘*capito*-complex’’ is the $2n = 58–60$, $FN = 62–66$ population identified as *O. yunganus.* This species is nearly identical with *O. capito,* especially externally, but may be distinguished by the comparatively narrow incisive foramina and the presence of an enamel island in the second upper molars separating the first primary and major folds (first internal fold discrete). These molars differ from those of *O. nitidus* (another species with enamel islands) in that the first internal fold is usually coalesced with medial portions of the first secondary fold. While also superficially similar to *O. nitidus* in the shape of the incisive foramina, *O. yunganus* differs from both *O. nitidus* and *O. capito* in smaller overall size and a marked tendency for lateral as well as medial development of palatal excrescences.

Since 1976, the uniqueness of *O. yunganus* has been recognized by its treatment as a species in taxonomic papers (Musser and Williams, 1985); regional faunal reports for Venezuela (Ochoa et al., 1988a), Ecuador (Albuja, 1991), and Perú (Malygin, 1994; Woodman et al., 1991; Woodman et al., 1995); and in general checklists (Musser and Carleton, 1993). However, the boundaries of its morphological variation and geographic range have never been defined. That is our purpose here. We provide a gazetteer of collection localities for *O. yunganus* that includes specimens examined. We delineate the geographic distribution as indicated by those localities, summarize trapping and ecological data from several localities as examples of the habitat in which *O. yunganus* was encountered, document sympatry between *O. yunganus* and other species in the former *O.* ‘‘*capito*’’ complex, describe the characteristics of *O. yunganus* and contrast them with samples of related species in the former *O.* ‘‘*capito*’’ complex, and present analyses of morphological variation among samples of the species within a geographic framework.

We also name and describe a new species related to *Oryzomys yunganus.* During the early phase of our specimen survey, when we were sorting through collections in museums and identifying specimens with the morphological traits characteristic of *O. yunganus* as defined by Thomas (1902) and Gardner and Patton (1976), we encountered 12 specimens that exhibited features outside the range of variation we had previously found. All 12 are large, which is not unusual (large body size also characterizes many other samples from western Amazonia and eastern Venezuela), but they possess darker pelage, much longer toothrows, and more massive molars than we had seen in the other samples, and they differ significantly in some cranial traits. The material was collected by G.H.H. Tate between 1158 and 1524 m in wet forest at Mirador, Palmera, and Mera (localities 25–27 in the gazetteer) on the eastern Andean slopes in central Ecuador. We treated these specimens as just another sample in our multivariate analysis of geographic variation of morphological characters in *O. yunganus.* Results of principal components and discriminant function analyses reflected our initial observations of skins and skulls; although considerable intersample variation is present among all the samples analyzed, the specimens from Mirador, Palmera, and Mera are consistently isolated from all other samples in all multivariate results. This separation is even more significant because samples of what we regard as good *O. yunganus* come from nearby localities in Ecuador at both high and low elevations and from the Andean slopes of Perú at elevations exceeding those in the Palmera region. All the data support the conclusion that the 12 specimens represent a different gene pool, a species distinct from but related to, *O. yunganus*. We exclude these 12 rats from the following sections on geographic distribution, habitat, sympatry, and comparisons with other species. We include them in the treatment of geographic variation within *O. yunganus* (identified simply as the ‘‘Palmera Sample’’) and there document their contrasts with the other samples. The new species is named and described following the account of *O. yunganus*.

GAZETTEER AND SPECIMENS

Listed below are the localities at which the 477 specimens we identify as *Oryzomys yunganus*, as well as those in the Palmera Sample (localities 25–27), were collected. The number preceding each place corresponds to the same numbered locality on the map in figure 14. We do not list any material that we did not personally examine.

FRENCH GUIANA

Arrondissement Cayenne

1. **Arataye** (spelled Arataï in USBGN French Guiana, 1993: 7; either ‘‘Arataye’’ or ‘‘Réserve de l’Arataye’’ is written on skin tags); specimens taken at Saut Pararé, an ‘‘Ecological Station of the Muséum National d’Histoire Naturelle,’’ on the left side of the Crique (River) Arataye, 04°02′N/52°42′W (Dubost, 1988: 108), 40 m (Voss and Emmons, 1996: 95): MNHN 1986-294, 1986-297, 1986-313, 1986-881, 1986-883.
2. **Kaw** (on Rivière de Kaw near end of Canal de Kaw; Stephens and Traylor, 1985: 7), 04°29′N/52°02′W, 100 m: MNHN 1986-490.
3. **Île de Cayenne**, which is a ‘‘sea level ‘island’ ca. 20 km by 8 km, defined by Fleuve Mahury, Rivière du Tour de l’Île and the Atlantic Ocean; Cayenne city is on NW end’’ (Stephens and Traylor, 1985: 3); includes **Rorota;** 04°50′N/52°20′W: MNHN 1986-322, 1986-324, 1986-326, 1986-327, 1986-800, 1986-801, 1986-802, 1986-803.
4. **Cacao**, which is ‘‘on right bank of Rivière Comté, ca. 20 km above its mouth’’ (Stephens and Traylor, 1985: 2), 04°35′N/52°28′W, 24 m: MNHN 1986-490.
5. **Paracou (Domaine Experimental Paracou), 15 road km SSE Sinnamary and 50 road km WNW Kourou**, 05°17′N/52°55′W, 10–45 m (R. S. Voss, personal commun.): AMNH 266495, 266496, 266500, 266503, 266510–266513, 266516, 266517, 266520, 266522, 266524, 266526, 266531, 266532, 267017, 267567.

SURINAM

District Marowijne

6. **4 km N, 10 km W Albina,** 05°30′N/54°03′W (CM mammal catalog), on coastal plain: CM 54060, 54061.
7. **Mongotapoe, Wia-wia bank,** ‘‘coastal plain on upper Coermotibo River’’ (Stephens and Traylor, 1985: 83), 05°35′N/54°15′W: RMNH 16054.

District Surinam

8. **Powakka,** ‘‘ca. 50 km S of Paramaribo’’ (Stephens and Traylor, 1985: 88), 05°27′N/55°05′W, on coastal plain: CM 54048, 54063–54065.

District Para

9. **Groot Poika** (also written Bigi Poika or Poka), **Acarami Creek**, ‘‘coastal plain, between Coesewijne and Saramacca rivers’’ (Stephens and Traylor, 1985: 76), 05°25′N/55°30′W: CM 54062.

District Sipaliwini

10. **Tafelberg, SE side of Arrowhead Basin, Augustis Creek**, 03°54′N/56°10′W (Williams et al., 1983: 331), 600 m: CM 76926–76931. **Tafelberg, Geyskes Creek,** 03°56′N/56°10′W (Williams et al., 1983: 331), 700 m: CM 76933, 76936. **Tafelberg, Lower Geyskes Creek,** 03°56′N/56°11′W (CM mammal catalog): CM 76937.
11. **Kaiser Gebergte (Kaiserberg) Airstrip, Zuid River,** 03°06′N/56°28′W (Genoways et al., 1981: 325), 275 m: FMNH 93284, 93286.

GUYANA

District Barima-Waini

12. **Kwabanna**, 07°34′N/59°09′W (M. Engstrom, personal commun.), 1–100 m: ROM 98719, 98730, 98738, 98747.
13. **Santa Cruz**, 07°40′N/59°14′W (M. Engstrom, personal commun.), 1–100 m: ROM 98771, 98781, 98782, 98824–98826.

VENEZUELA

Estado de Bolívar

14. **Auyán Tepuy** (the current and correct spelling according to USBGN Venezuela, 1993: 32; spelled Auyán-tepui or Auyán Tepuí in most other gazetteers and atlases), a ‘‘very large

sandstone table mountain, with summit area of 700 sq. km and 200 sq. km. of talus slopes, in east-central Bolívar, on right side of Río Caroní'' (Paynter, 1982: 13; see Tate, 1938, and Gilliard, 1941, who describe the region and location of collection camps), 05°45′N/62°30′W, 1100 m: AMNH 130896, 130898, 130899, 130901–130903, 130905, 130906, 130914–130916, 130921, 130932–130934, 130937, 130940, 130941, 130943, 130948, 130952, 130955, 130959, 130960, 130962, 131096, 131101, 131104, 131125–131127.

15. **Arabopó** (Arabupu on skin tags), ''8 mi SE of Monte Roraima on Río Arabopó which rises on Roraima, savanna, with subtropical forest beginning short distance N'' (Paynter, 1982: 8; also see Tate's [1930] description of region and camps, as well as his account of life zones [Tate, 1932c]), 05°06′N/60°44′W, 4200 ft: AMNH 75770.

Estado de Amazonas

16. **Cerro Duida, Agüita Camp**, ''on southeastern slope of Cerro Duida close above Caño Seco, heavy forest, transition between tropical/subtropical zones'' (Paynter, 1982: 2; also see Tate and Hitchcock, 1930; Gleason, 1931; Dezzeo and Huber, 1995), 03°20′N/65°32′W, 3250 ft: AMNH 77314, 77337.
17. **Tamatama, Río Orinoco, ''2 km above mouth of Brazo Casiquiare,''** Handley, 1976: 84), 03°10′N/65°49′W, 135 m (Handley, 1976: 84): USNM 409869, 409872.

COLOMBIA

Departamento de Cundinamarca

18. **Guaicaramo** (also spelled Guaycaramo on skin tags), which refers to ''hills . . . at eastern base of Eastern Andes, where boundaries of Boyacá, Cundinamarca, and Meta [and Casanare] meet'' (Paynter and Traylor, 1981: 96), 04°43′N/73°02′W: AMNH 71328.

Departamento del Meta

18a. **Villavicencio,** at ''eastern base of central Eastern Andes and on western edge of Llanos, on Río Guatiquía'' (Paynter and Traylor, 1981: 274), 04°09′N/73°37′W, 500 m: AMNH 136357.

18b. **Serranía de La Macarena,** an ''isolated, boat-shaped sandstone chain, ca. 125 km long and 30 km wide, with a maximum altitude of 5500 ft., at Pico Renjifo'' (Paynter and Traylor, 1981: 132), 02°45′N/73°55′W; **Pico Renjifo,** 4500 ft: FMNH 87969, 87970. **Camp Izawa, El Parque La Macarena:** FMNH 58778, 58779.

Intendencia del Putumayo

19. **Río Mecaya, at the Río Caquetá** (see Paynter and Traylor, 1981: 157), 00°28′N/75°20′W, 185 m: FMNH 72067.

Intendencia del Caquetá

20. **Tres Troncos,** on the ''left bank of Río Caquetá, 60 km NW of junction of Río Caguan with the Caquetá'' (Paynter and Traylor, 1981: 262), 00°08′N/74°41′W, 185 m: FMNH 72036, 72051, 72066.

ECUADOR

Provincia de Napo

21. **San Francisco, Aguarico,** 00°30′S/76°22′W, 200 m: UMMZ 80117, 80118, 80133, 80135–80139.
22. **Llunchi,** ''an island about 18 km below mouth of Río Coca'' (Hershkovitz, 1944: 98), 00°37′S/76°46′W, 250 m: UMMZ 80095, 80106-80108.
23. **San José Abajo** (this is the notation on skin tags [translates lower San José]; Chapman, 1926: 719, refers to the place as ''San José de Sumaco; Paynter and Traylor, 1977: 110, explained why they call it ''San José Nuevo; Chapman, 1926: 719, also explained ''that all American Museum specimens recorded from 'San José' or 'below San José' are from or near San José de Sumaco''), 00°26′S/77°20′W, 250 m: AMNH 64023, 64024, 66796, 68049, 68059, 68082, 68105, 68106, 68115.
24. **Volcán Sumaco** (= lower [abajo] Sumaco; see Paynter and Traylor, 1977: 119), 00°34′S/77°38′W: AMNH 68118.

Provincia del Tungurahua

25. **Mirador, 15 mi E Baños,** ''on Baños-Canelos trail, N bank of Río Pastaza, W of Río Mapota'' (Paynter and Traylor, 1977: 75), 01°26′S/78°15′W, 5000 ft: AMNH 67357.
26. **Palmera** (also spelled Palmira), a hacienda ''on the south bank of the Río Pastaza approached by a cable bridge over the river about a kilometer east of Hda. Santa Ines'' (Brown, 1941: 840); Tate could see ''Palmera, my next camp. Ten miles away'' (field journal, AMNH Mammalogy Archives), 01°25′S/78°12′W, 4000 ft: AMNH 67358–67365, 67376.

Provincia de Pastaza

27. **Mera,** which is ''on the high terraces just north of the Rio Pastaza where that river leaves the eastern foothills of the Andes'' (Brown, 1941: 834), 01°28′S/78°06′W, 1160 m (coordinates and elevation from Paynter and Traylor, 1977: 74): AMNH 67366, 67367.
28. **Río Yana Rumi** (= Río Yanarumiyacu), 01°38′S/76°59′W (USBGN Ecuador, 1987: 366): FMNH 43265.
29. **Río Capahuari**, a tributary of the Río Pastaza, 01°55′S/77°20′W (Hershkovitz, 1960: 565), or ''left-bank tributary of middle Río Pastaza meeting that river near Ecuador/Perú border, 02°31′S/76°51′W'' (Paynter, 1993: 29): FMNH 43268, 43270, 43271.

30. **Río Tigre,** ‘‘a town on Ecuador-Perú border where Río Conambo and Río Pindo join to form Río Tigre, a major tributary of the Amazon’’ (Paynter and Traylor, 1977: 103), 02°07′S/76°04′W (‘‘76° W, 2° S’’ are the coordinates noted on skin labels), 1000 and 2000 ft: BMNH 54.431–54.434, 54.436.

Provincia de Zamora-Chinchipe

31. **Zamora** (see Paynter, 1993: 225; Hershkovitz, 1960: 566, who gives slightly different coordinates; Chapman, 1926: 722), 04°04′S/78°58′W, 3250 ft: AMNH 47830.

PERÚ

Departamento de Loreto

32. **Boca del Río Curaray** (see Stephens and Traylor, 1983: 64, 02°22′S/74°05′W, 140 m: AMNH 71570.
33. **Huachi,** which is on the Río Pastaza, 03°25′S/76°20′W (coordinates from Hershkovitz, 1977), 1500 ft: BMNH 54.421, 54.422, 54.425–54.430, 54.443.

Departamento de Amazonas

34. **Mouth of Río Santiago,** which ‘‘flows south to left bank of Río Marañón’’ (Stephens and Traylor, 1983: 201), 04°27′S/77°38′W: AMNH 98257.
35. **Yambrasbamba,** 05°45′S/77°54′W, 6500 ft: BMNH 26.8.6.16; UMMZ 82978, 82979.
36. **Yambra, 10 m N Corosha,** 05°50′S/77°45′W (for Corosha, USBGN Perú, 1955), 6500 ft: BMNH 26.8.6.14, 26.8.6.15; UMMZ 82978.

Departamento de San Martín

37. **Uscho (= Uchco), 50 m E Chachapoyas,** ‘‘uncertain whether in [Departamento de] San Martín or [Departamento de] Amazonas, but apparently on left bank of Río Huallaga drainage’’ (Stephens and Traylor, 1983: 227), 06°11′S/77°13′W, 5000 ft: AMNH 73182, 73183.
38. **Puca Tambo,** ‘‘on trail from Chachapoyas to Moyobamba, Río Huallaga drainage’’ (Stephens and Traylor, 1983:170), 06°10′S/77°16′W, 5100 ft: FMNH 19787; BMNH 26.5.3.31–26.5.3.42.
39. **Rioja,** ‘‘ca. 20 km W of Moyobamba’’ (Stephens and Traylor, 1983: 184), 06°05′S/77°09′W, 842 m: USNM 259607.
40. **Moyobamba,** ‘‘on upper Río Mayo (Stephens and Traylor, 1983: 139), 06°03′S/76°58′W, 2800 ft: FMNH 19376, 19387, 19392, 19393.

Departamento de Huánuco

41. **Río Pachitea,** a ‘‘large tributary to left bank of Río Ucayali’’ (Stephens and Traylor, 1983: 151), 08°46′S/74°32′W: BMNH 23.10.16.34.
42. **Cerros del Sira,** 1120 m, 09°28′S/74°46′W: AMNH 242330.
43. **Río Chinchao, Hacienda Buena Vista,** ‘‘on Río Chinchao, a few km above Vista Alegre’’ (Stephens and Traylor, 1983: 22), 09°30′S/75°56′W, 3500 ft: FMNH 24544–24553.
44. **Chinchao,** ‘‘on upper Río Chinchao; subtropical zone’’ (Stephens and Traylor, 1983: 48), 09°38′S/76°04′W, 5700 ft: FMNH 23721, 23722.

Departamento de Pasco

45. **Pozuzo** (formerly within Departamento de Huánuco border), ‘‘on Río Pozuzo, Ucayali drainage, left bank’’ (Stephens and Traylor, 1983: 168), 10°04′S/75°32′W, 1000 m: FMNH 126707; MCZ 27019.
46. **San Pablo,** an ‘‘Indian village on E bank of Río Azupizu, virgin evergreen forest’’ (Stephens and Traylor, 1983: 196), 10°27′S/74°52′W, 900 ft: AMNH 231666.
47. **Eneñas** (see Stephens and Traylor, 1983: 69), 10°45′S/75°14′W, 5000 ft: BMNH 28.5.1.8, 28.5.1.9, 28.5.1.11, 28.5.1.13, 28.5.1.14.

Departamento de Junín

48. **Perené** (= Valle Perené, Colonia del Perené), a ‘‘coffee plantation at junction of ríos Paucartambo and Chanchamayo’’ (Stephens and Traylor, 1983:161), 10°58′S/75°13′W, 1000 m: AMNH 61816.

Departamento de Ucayali (formerly part of Departamento de Loreto; ‘‘in 1980 the former department of Loreto was divided into two departments, Loreto in the north and Ucayali in the south,’’ Stephens and Traylor, 1983: iv).

49. **Balta,** a ‘‘small Cashinahua Indian Village on the Río Curanja, a tributary of the Río Alto Purús’’ (Gardner and Patton, 1976: 42; also see Voss and Emmons, 1996: 103, as well as Duellman and Thomas, 1996: 3, for general descriptions of the Balta site), 10°06′S/71°14′W, 300 m: LSUMZ 16685, 16687, 16689; MVZ 136585, 136587.

Departamento de Madre de Dios

50. **Reserva Cuzco Amazónico**, a wildlife reserve consisting ‘‘of 10,000 ha at an elevation of about 200 m above sea level on an alluvial plain on the north bank of the Río Madre de Dios, about 15 km east-northeast of the town of Puerto Maldonado, Provincia de Tambopata’’ (Duellman and Koechlin, 1991: 5), 12°33′S/69°03′W, 200 m: KU 144519–144522.

Departamento de Ayacucho

51. **San José, on Río Santa Rosa,** which is a ‘‘small settlement a short distance below Huanhuachayo [this place, according to Gardner and Patton, 1976: 42, is a ‘‘clearing along the Andean mule trail connecting Hacienda Luisiana and nearby communities along the Río Apurimac and Río Santa Rosa with the

mountain town of Tambo''] on the Río Santa Rosa'' (Gardner and Patton, 1976: 43), 12°44′S/73°46′W, 3300 ft: LSUMZ 16685, 16687, 16689.

Departamento de Cuzco

52. **Santa Ana,** ''a few km SW of Quillabamba on Río Urubamba'' (Stephens and Traylor, 1983: 198), 12°52′S/72°43′W, 3500 ft: USNM 94887.
53. **Quincemil** (also spelled Quince Mil), ''on left bank of Río Marcapata'' (Stephens and Traylor, 1983: 180), 13°16′S/70°38′W, 680 m: FMNH 75242, 75253, 75254, 75257, 75259, 75261–75264, 75272.
54. **Cadena** ''in Río Marcapata valley; Kalinowski's farm, usually called Hacienda Cadena in the literature'' (Stephens and Traylor, 1983: 25), 13°24′S/70°43′W, 1000 m: BMNH 4.12.4.11, 4.12.4.12; FMNH 68630, 68631, 66401, 65704, 65707, 66399.

Departamento de Puno

55. **Río Inambari** (Linimbare is the variant written on skin tag). The specimen was collected by P. O. Simons at 1000 m on July 19, 1900; Stephens and Traylor (1983: 98) suggested that during July Simons was ''probably near Oroya'' at 13°53′S/69°40′W (Stephens and Traylor, 1983:148), which places it in Departamento Puno, not Madre de Dios as those authors indicate. BMNH 1.1.1.26.

BOLIVIA

Departamento de Pando

56. **Las Piedras,** 11°02′S/66°07′W, 170 m: AMNH 262736.

Departamento del Beni

57. **Boca del Río Biata**, 11°44′S/66°47′W, 170 m: AMNH 262950—262952, 262957.

Departamento de La Paz

58. **Bella Vista,** ''central La Paz, 10 km SSW of Mapiri'' (Paynter, 1992: 10), 15°20′S/68°13′W, 1400 m: BMNH 1.1.1.65. This is the only example known from La Paz and one of the two Thomas (1902: 130) referred to as being ''closely similar to [*O. yunganus*]'' and ''previously obtained by Mr. Simons near Mapiri''. Yensen et al. (1994: 407) recorded a specimen of *O. yunganus* (Colección Boliviana de Fauna 2313) from 1 km south of La Reserva (15°44′S/67°31′W) in the Departamento. Occlusal pattern of second upper molars in that individual is like *O. yunganus* but it also has squamosoalisphenoid grooves (Sydney Anderson, personal commun.); that combination of traits is typical of *O. nitidus*, which is common at La Reserva (see locality 86 in gazetteer for *O. nitidus*), and 2313 is most certainly an example of that species and not *O. yunganus.*

Departamento de Cochabamba

59. **Charuplaya,** 16°36′S/66°37′W (see the discussion under *O. yunganus* in Taxonomic Summary, which explains our reasons for locating Charuplaya at these coordinates), 1350 m (taken from skin tag): BMNH 2.1.1.39 (holotype of *Oryzomys yunganus*).

Departamento de Santa Cruz

60. **4.5 km N and 1.5 km E Cerro Amboró, Río Pitasama,** 17°45′S/63°40′W, 620 m: AMNH 262079, 262081; MSB 56001.

BRAZIL

Estado do Acre

61. **Sena Madureira** (Km 8 on Route BR 364 between Sena Madureira and Manuel Urbano), 09°05′S/68°41′W, 100–200 m: USNM 545296, 545300, 545302, 545304.
62. **Opposite Igarapé Porongaba, left bank Rio Juruá,** 08°40′S/72°47′W (these and all other coordinates of localities along the Rio Juruá are from a copy of J. L. Patton's field notes), below 400 m: MNFS 1172, 1181, 1240, 1347, 1389, 1406.
63. **Igarapé Porongaba, right bank Rio Juruá,** 08°40′S/72°47′W, below 400 m: MNFS 1093, 1101, 1128, 1171, 1323.
64. **Ocidente, right bank Rio Juruá,** 08°34′S/72°48′W, below 400 m: MNFS 1004.
65. **Sobral, left bank Rio Juruá,** 08°22′S/72°49′W, below 400 m: MNFS 1455.
66. **Nova Vida, right bank Rio Juruá,** 08°22′S/72°49′W, below 400 m: JUR 212, 214, 227; MNFS 1588, 1650.

Estado do Amazonas

67. **Seringal Condor, left bank Rio Juruá,** 06°45′S/70°51′W, below 400 m: JLP 15257, 15523, 15535, 15571, 15605, 15720, 15721; MNFS 527, 528, 553.
68. **Penedo, right bank Rio Juruá,** 06°50′S/70°45′W, below 400 m: JLP 15250, 15262, 15263, 15265, 15266, 15275, 15281–15283, 15288–15290, 15312, 15319, 15321, 15323–15329, 15361, 15476, 15480, 15495, 15500, 15519; MNFS 335, 341, 349, 367, 368, 384, 386–388, 390–392, 412, 511, 519, 521.
69. **Igarapé Nova Empresa, left bank Rio Juruá,** 06°48′S/70°44′W, below 400 m: JLP 15415, 15446; JUR 2, 5, 7, 8, 13, 35, 37, 38, 41, 45, 46, 73–75, 110; MNFS 484.
70. **Opposite Altamira, left bank Rio Juruá,** 06°35′S/68°54′W, below 400 m: MNFS 918.
71. **Altamira, right bank Rio Juruá,** 06°35′S/68°54′W, below 400 m: JLP 16021, 16068.
72. **Barro Vermelho, left bank Rio Juruá,** 06°28′S/68°46′W, below 400 m: JLP 15784, 15830; MNFS 778.
73. **Jainú, right bank Rio Juruá,** 06°28′S/68°46′W, below 400 m JLP 15759; MNFS 697.

74. **Colocação Vira Volta, on Igarapé Arabidi, affluent of Paraná Breu, left bank Rio Juruá,** 03°17′S/66°14′W, below 400 m: JUR 440, 445, 463, 464, 474, 475, 483, 489, 494, 509, 524, 543, 557.
75. **Colocação das Antas, left bank Rio Riozinho** (approx. 46 km N Carauari), 04°28′S/66°53′W (J. Malcolm, personal commun.), 0–100 m: NC 6002 (J. Malcolm).

Estado de Rondônia

76. **Rio Roosevelt**, which is a ‘‘major affluent on left bank of upper Rio Aripuanã . . . that rises in extreme northeastern Rondônia and flows through extreme northwestern Mato Grosso and reaches the Aripuanã in southeastern Amazonas (ICWB); formerly known as ‘Rio da Duvida’ but that name now restricted to a headwater [at 11°57′S/60°20′W]. . . .’’ (Paynter and Traylor, 1991: 529). The specimen was collected on February 27, 1914, by L. E. Miller, who was a member of the Roosevelt-Rondon Scientific Expedition; ‘‘Rio Duvida’’ is written on the skin tag. Roosevelt (1914: 243) recounted that February 27 was when the expedition started down the ‘‘River of Doubt’’ (Rio Duvida). The camp, which they broke shortly after midday, was located at ‘‘about 12°1′ latitude south and 60°15′ longitude west of Greenwich’’ at the ‘‘Telegraph Road Bridge’’ (as indicated on the detailed map of the Rio Roosevelt, which is a supplement to the account by Roosevelt, 1915a). Miller (1915: 63) provided a photograph of the expedition party loading canoes for its journey down the river from the bridge, and the forest in the background. Ornig (1994: fig. 43) also illustrated the telegraph bridge, the river, and tall forest from another perspective (also see fig. 16); 200–500 m: AMNH 37113.

Estado do Mato Grosso

77. **Rio Saueniná**, a ‘‘tributary in southwestern Mato Grosso on left side of Rio Sauêruiná’’ (Paynter and Traylor, 1991: 596). The specimen listed below is another obtained during the Roosevelt-Rondon Scientific Expedition, and was collected on February 8, 1914, by L. E. Miller from ‘‘Maracana,’’ which Miller (1924: 14) referred to as the ‘‘Maracana River.’’ Paynter and Traylor (1991: 596–597) indicated that the Maracana River is now called the Rio Saueniná, and noted that G. K. Cherrie (another member of Roosevelt’s expedition) and Miller were there on February 7, 1914; 12°24′S/58°40′W, 200–500 m: AMNH 37112.
78. **Serra do Roncador, 264 km (by road) N Xavantina** (biological and geographic information about this site are provided in Pine et al., 1970, Brown et al., 1970; Askew et al., 1970, Ratter et al., 1973, and Bishop, 1974), 12°49′S/51°46′W (from Pine et al., 1970), 400 m: BMNH 81.470, 81.472, 81.473, 81.518–81.523, 81.525, 81.531–81.541, 81.543-81.549, 81.554, 81.569, 81.570, 81.572–81.580, 81.591, 81.593, 86.1132–86.1134, 86.1138, 86.1147, 87.637.

Estado de Pará

79. **54 km S, 150 km W Altamira** (Gleba 61 Lote 02), 03°40′S/52°45′W, below 200 m: USNM 521527.
80. **18 km S, 19 km W Altamira** (Agrovila da Uniao, Km 43 on the Trans-Amazonian Highway between Altamira and Itaituba), 03°22′S/52°35′W, below 200 m: USNM 521444, 521445, 521519, 521521.

Estado do Amapá

81. **Serra do Navio, Macapá,** 00°02′N/51°05′W, 0–100 m: USNM 392065, 392070.
82. **Serra do Navio, Rio Amapari:** USNM 393886, 393893, 393895, 393901, 393913, 393915, 393916, 393918, 393951, 393961, 393969, 393979, 394021, 394022, 394041–394043, 394050, 394052, 394059, 394105, 394106, 394109, 394192. **Terezinha:** USNM 393865, 393866, 393868, 393869, 393871, 393872, 393877, 393878. **Serra C3:** USNM 393905, 393910, 393946, 393988, 394006, 394044. **Estrada de Ferro Amapá, Km 190:** USNM 393899, 394074, 394076, 394108, 394117, 394119, 394148, 394152, 394162, 394167, 461525. Localities were obtained from a map of arbovirus research stations published in the 1966 Annual Report of the Belém Virus Laboratory (files of Mammal Division, National Museum of Natural History); 00°59′N/52°03′W, 0–100 m.

ORYZOMYS YUNGANUS Thomas, 1902

DISTRIBUTION AND HABITAT

Oryzomys yunganus occurs throughout a vast region designated as Amazonia (fig. 15), which according to Haffer (1987a: 111) ‘‘comprise[s] the Amazon Basin as well as the Guianas and southern to eastern Venezuela (southern part of the Orinoco drainage).’’ The extent of Amazonian rain forest has also been classically defined by Ducke and Black (1953: 1–2): ‘‘The Hylaea of Humboldt and Bonpland is the great equatorial rain forest of South America covering most of the Amazon basin, the basin of the upper Orinoco, the Guianas, and the basins of the lower Tocantins including the Rio Pará and the small rivers of the Atlantic drainage eastwards to the Rio Turiassú in the State of Maranhão.'' Generally similar versions of ''Amazonia'' have been illustrated by Dixon (1979), Connor (1986), Van der Hammen (1974), and Voss and Emmons (1966). Ab'Sáber's Equatorial Amazonian Morphoclimatic Domain is roughly equivalent to most outlines of Amazonia (see Heyer, 1988: 266). Distribution of collection localities for *O. yunganus* (fig. 14) is in the Amazon Basin of southern Colombia, Ecuador, Perú, Bolivia, and Brazil; the southern drainage basin of the Río Orinoco in northeastern Colombia and southern Venezuela (also see Ochoa et al., 1993); and the Guiana Region from the tepuis of eastern Venezuela through Guyana, Surinam, French Guiana, and the Amapá area of Brazil. Longitudinal boundaries, as defined by provenances of specimens examined, extend from foothills of the Ecuadoran Andes at Zamora (locality 31, longitude 78°58′W) east to Brazil at Macapá (locality 81, longitude 51°05′W) in Amapá north of the delta of the Rio Amazonas/Solimões, and at Serra do Roncador (locality 78, longitude 51°46′W) in Mato Grosso south of the Amazon River. Known latitudinal limits are defined by Santa Cruz (locality 13, latitude 07°40′N) in northern Guyana, and near Cerro Amboró (locality 60, latitude 17°45′S) in Santa Cruz, Bolivia. Although recorded from a few localities (14–17) east and south of the Río Orinoco in Venezuela, *O. yunganus* has not been collected in the Orinoco delta or north of the Río Orinoco in the forests of northeastern Venezuela, nor has it been taken in western Venezuela along the forested strip between foothills of the Cordillera de Mérida and the Llanos of the Orinoco (the geographic relationship of forest and Llanos can be visually appreciated by the maps in Hueck and Seibert [1981] and Voss [1991: 86]).

Oryzomys yunganus occupies a wide altitudinal bracket within Amazonia. Elevations of collection localities range from 1982 m at Yambra and Yambrasbamba in foothills of the Peruvian Andes to near sea level in French Guiana. Most sites in the Guianas and Amazon Basin are below 600 m; higher sites of collections are on slopes of the tepuis in eastern Venezuela, on the isolated Serranía de la Macarena in Colombia, and along the Andean foothills in Ecuador and Perú.

Habitat information tied to specimens is scanty but indicates that most examples of *O. yunganus* have been collected in tropical evergreen rain forest, both primary and secondary formations, but some were also captured in habitats representing human alterations of the original forest; no records come from savanna habitats. The information we have been able to glean from specimen labels, field notes, unpublished manuscripts, publications, and speaking with collectors is summarized below by country.

FRENCH GUIANA: We have notes for two localities at which samples of *O. yunganus* were collected, **Saut Pararé**, the field station in the lower Arataye basin (locality 1) and **Paracou** (locality 5). Dubost (1988: 108) wrote that Saut Pararé

> comprises 16,700 ha of uninhabitated lowland evergreen rainforest characterized by a predominance of Burseraceae, Chrysobalanaceae and Lecythidaceae. . . . Mean monthly temperature varies little (25.8° C to 27.3° C). Rainfall is high (mean 3700 mm per year). There is a pronounced dry season from July to November (mean monthly rainfall: 85–250 mm), and a long rainy season covering the rest of the year (mean monthly rainfall: 325–560 mm), interrupted by a short dry season (February–March) which is often irregular or poorly marked.

Specimens from Paracou were trapped by R. S. Voss and members of his survey team. Detailed habitat information will eventually be published by them; meanwhile, Voss told Musser that all the animals came from primary rainforest habitats and also noted (Voss, unpubl.) that

> Six years of weather records from Sinnamary (about 15 km NNW of the study area) document an average annual rainfall of 2886 mm and a distinctly seasonal pattern of precipitation. . . . Heavy rains that usually begin in mid-December and extend through early July account for over three-quarters of the annual total precipitation; rainfall in the four driest months (August through November) accounts for less than ten percent. Two shaded thermometers installed 1.3 m above the ground in primary forest near our camp from 17 July to 28 August 1991 recorded a 24-hour average maximum temperature of 27.3°C and an average minimum of 22.5°C.

VENEZUELA: Very general information is available for two locations. A large series of *O. yunganus* was obtained from **Auyán Tepuy** (locality 14) by G.H.H. Tate and J. A. Dillon from a camp made at 1100 m. All were originally identified as ''*O. laticeps ve-*

lutinus'' by Tate, who (1939: 189), in his account of *O. macconnelli,* wrote that ''These fine, large *Oryzomys* [*macconnelli*] were trapped only in forest. They were very much scarcer than *Oryzomys laticeps* which occupied the same environment.'' Tate (1938: 474) listed the ''1100-meter camp'' with this short description: ''Altitude, corrected by Jahn, 1038 meters. Savannas, outcrops of nearly flat sandstone. Dense forest representing junction of lower subtropics and upper tropics. Occupied continuously from December 2, 1937, to February 28, 1938.'' Tate's field journals did not elaborate significantly beyond these statements.

One *O. yunganus* and 34 *O. megacephalus* were collected at 1280 m near **Arabopó** at the base of Mt. Roraima (locality 15 in gazetteer) by G.H.H. Tate during December 1927 and January 1928. Tate (in his journal of ''Distribution and Ecological Notes of Roraima Expedition,'' AMNH Mammalogy Archives) noted that ''all the *Oryzomys* from the camp at 4200 feet were taken in the Weitipu forest.'' Aerial and interior views of that forest were provided by Tate (1932c: 241–242), as were sketchy descriptions.

Two specimens come from **Tamatama** (locality 17), which, as described by Handley (1976: 84), is on the ''Undulating plain of Río Orinoco, with hills up to 60 m. High evergreen forest, more or less disturbed near river. Most collecting in thatched roofed buildings, yards, and gardens of New Tribes Mission. Holdridge classification: TROPICAL humid forest (bh-T).''

PERÚ: Notations on labels of specimens collected by R. W. Hendee in 1926 and 1927 reveal the following: **Yambrasbamba** (locality 35), ''trapped at edge of river in forest''; **Yambra** (locality 36), one rat was ''trapped by rocks in palm grove,'' another was ''trapped in heavy forest''; **Puca Tambo** (locality 38), four rats were ''trapped in sweet potato field,'' one was ''trapped under log in field,'' and six were ''trapped in forest''; **Eneñas** (locality 47), all were ''trapped in deep forest.''

Specimens from **Cuzco Amazónico** (locality 50) were collected in both wet and dry seasons in ''floodplain forest'' and ''floodplain forest adjacent to seasonally inundated swamp forest'' (Woodman et al., 1995: 3). Descriptions of soil characteristics, rainfall patterns, and vegetation are provided by Duellman and Koechlin (1991).

A specimen collected by P. O. Simons in 1900 at **Río Inambari** (locality 55) was taken ''In deep wet wood'' according to notation on specimen label.

BOLIVIA: A specimen from **Bella Vista** (locality 58) collected in 1899 by P. O. Simons was trapped ''In old house.''

BRAZIL: The region north of Xavantina in the Serra do Roncador is a good example of habitat on the fringe of Amazonia. Specimens of *O. yunganus* were collected by members of an expedition sponsored by the Royal Society/Royal Geographic Society in cooperation with the National Research Council of Brazil and carried out during 1967–1969. Brown et al. (1970: 265) described the climate of the region as

> of the savanna type with a marked wet and a dry season. In 1968 the total rainfall of 1372 mm fell in 148 days, almost entirely between November and April. The mean monthly maximum temperature was 32.7° C and the mean monthly minimum 17.0° C. The rains included some exceedingly heavy downpours of short duration, the most intense measured being 75 mm in 8 hours.

Vegetation in the Xavantina area consists of forest (*mata*), savanna (*cerrado*), and grassland (*campo*). All 48 specimens of *O. yunganus* were collected in forest. Three came from a formation Askew et al. (1970: 213) referred to as ''dry forest,'' which merges with the wetter equatorial rain forest to the north of Xavantina, but near the base camp (**264 km N Xavantina**):

> covers both interfluves and valley sides . . . and consists of crowded, often slender trees of many different species of which no single one is dominant. These form an almost closed canopy so that ground vegetation is limited mainly to scattered tree seedlings. The forest becomes taller and more luxuriant northwards but a canopy height of 15–18 m, with the occasional emergent rising to 25 m, or more rarely to 30 m, is common in the base camp study area (264 km N Xavantina). Downslope towards the streams the canopy becomes somewhat lower before merging into gallery forest.

The rest of the specimens were captured in gallery forest, which Askew et al. (1970: 214) summarize this way:

> In Mato Grosso gallery or riparian forests, characterized by the presence of tall *Qualea* and *Sloanea* spp.,

Fig. 16. ‘‘Roosevelt’s canoe disappearing down Rio Téodoro, the River of Doubt. ‘Ahead of us the brown water street stretched in curves between endless walls of dense tropical forest’ ’’ (Roosevelt, 1915b: 35). That forest is also habitat of *Oryzomys yunganus* along the Rio Roosevelt (Rio da Duvida, locality 76 in gazetteer). Photographed in 1914 by L. E. Miller from the Telegraph Bridge near camp. Reproduced with permission from Theodore Roosevelt Collection, Harvard College Library.

TABLE 6
Contrasts in Length (in mm) of Dorsal Fur (Overhairs) between Sympatric Samples of *Oryzomys yunganus* and *Oryzomys megacephalus* from French Guiana, Guyana, and Venezuela

Locality[a]	*N*	M ± SD	Observed range
FRENCH GUIANA			
Paracou (5)			
O. yunganus	8	7.1 ± 0.64	6–8
O. megacephalus	12	6.0 ± 0.74	5–7
GUYANA			
Kwabanna (12) and Santa Cruz (13)			
O. yunganus	7	8.3 ± 1.11	7–10
O. megacephalus	5	5.4 ± 0.55	5–6
VENEZUELA			
Auyán Tepuy (14)			
O. yunganus	19	8.4 ± 0.60	7–9
O. megacephalus	40	6.6 ± 0.63	5–8

[a] Numbers key to numbered localities in gazetteer for *O. yunganus.*

> occur along the streamsides in both the cerrado and dry forest vegetation zones. The trees, the largest of which may reach a height of 40 m and a diameter of 2 m, often have well developed buttresses and surface roots. Compared with dry forest the gallery forest has a more dense ground vegetation. The width of the gallery may vary considerably depending on the valley form and consequent moisture regime. . . .

Detailed descriptions of vegetation and soils in the area covered by the expedition, including habitat photographs, forest profiles, vegetation maps, and other illustrative information, are provided in the reports by Askew et al. (1970) and Ratter et al. (1973).

The specimen taken at the headwaters of the **Rio Roosevelt**, or "River of Doubt" (locality 76), came from forest (fig. 16), and samples collected along the Rio Juruá were trapped in lowland tropical evergreen rainforest formations, which include undisturbed várzea and terra firme forest as well as second growth (J. L. Patton, personal commun., letter in AMNH Mammalogy Archives).

Description and Comparisons

Thomas's (1902) description of *O. yunganus* is accurate but not diagnosably useful without specimens of other species at hand for contrast. To adequately define *O. yunganus* requires comparisons with samples of *O. megacephalus, O. macconnelli,* and *O. nitidus.* Each one resembles *O. yunganus* in aspects of its morphology (so closely that some researchers in the field and museum regularly misidentified specimens of *O. yunganus* under each), the geographic range of each species broadly overlaps that of *O. yunganus,* and samples of all four species have been collected in different combinations at the same localities (see appendix G). We describe the morphological and chromosomal traits of *O. yunganus* within the context of comparisons first with *O. nitidus* and *O. macconnelli* (definitions of these species are provided in a later section), then with *O. megacephalus* (as we have defined the species in the previous account). Of the three, *O. yunganus* least resembles *O. nitidus,* and *O. macconnelli* and is most like *O. megacephalus.* That species and *O. yunganus* have similar geographic distributions, have been collected together at many localities, and consistently have been confused with one another.

Size of body and appendages: Adults of *Oryzomys nitidus* and *O. macconnelli* are conspicuously larger than *O. yunganus,* as indexed by lengths of head and body, hind foot, and tail in series collected at the same place (tables 8, 9, 14). The range in values for length of head and body overlap; however, ranges for lengths of tail and hind foot usually do not overlap between *O. macconnelli* and *O. yunganus* (samples from Auyán Tepuy, Venezuela, for example; table 8) and do so only slightly between the latter and *O. nitidus* (series from Balta, Perú; table 14).

Oryzomys yunganus and *O. megacephalus* are similar in body size (tables 8, 9, 14) but, judged by the sample from Auyán Tepuy, lengths of tail and hind feet of *O. yunganus* are shorter relative to length of head and body (fig. 24).

Coloration and texture of fur: Adults of *O. nitidus* and *O. macconnelli* clothed in prime pelage have lustrous tawny buff or reddish brown upperparts that are brighter along the sides of the body and slightly darker over the mid-dorsal region from nape to rump. *Oryzomys macconnelli* has long (up to 15 mm over the back and rump), lax fur

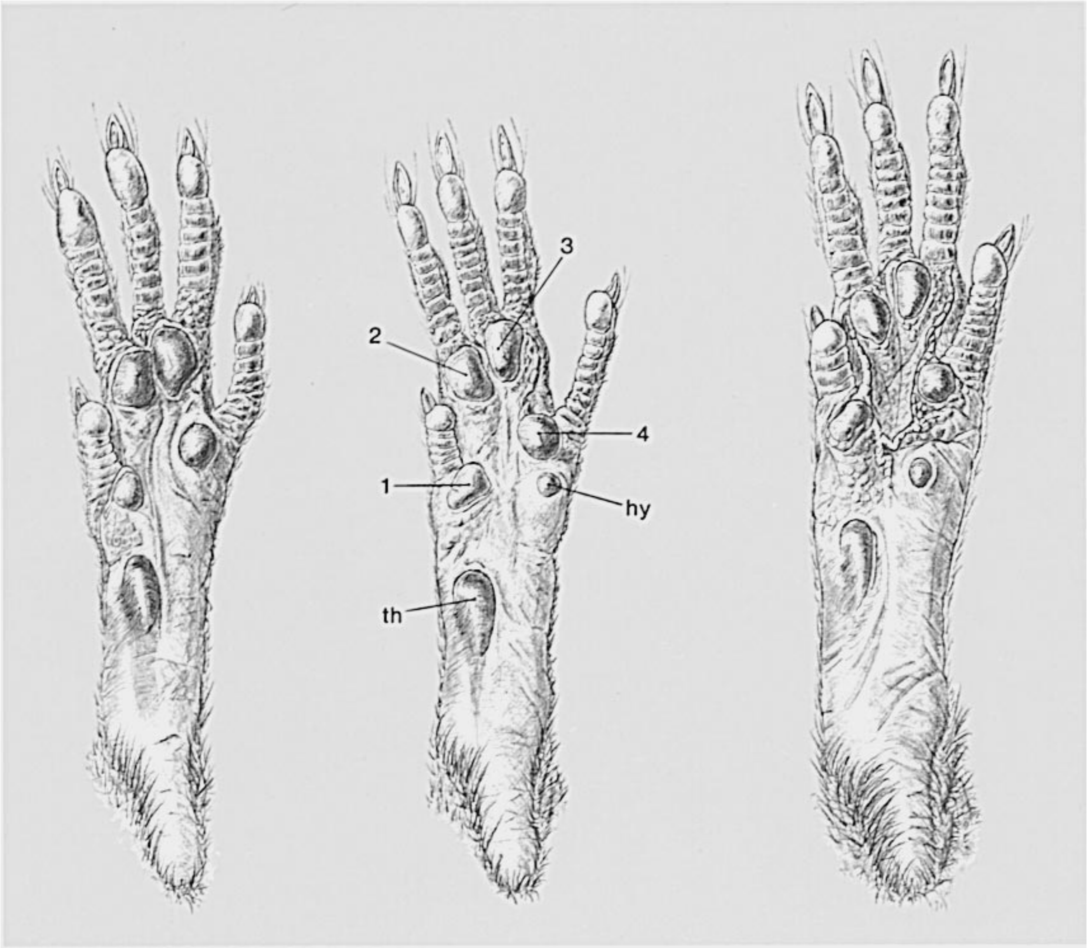

Fig. 17. Plantar views of left hind feet from adult *Oryzomys* illustrating variation in expression of the hypothenar pad (**hy**). **Left**: *O. yunganus* (AMNH 262081). **Middle**: *O. yunganus* (AMNH 262079). **Right**: *O. megacephalus* (AMNH 262080). Approximately ×5. All three specimens were collected 4.5 km N, 1.5 km E Cerro Amboró, Departamento de Santa Cruz, Bolivia (locality 60 in the gazetteer for *O. yunganus*). A few samples and individual specimens of *O. yunganus* lack a hypothenar pad (table 7); when present, the pad is often small. Nearly all of the hundreds of *O. megacephalus* we surveyed had the full complement of plantar pads: four interdigital pads (**1–4**), a thenar pad (**th**), and a large hypothenar.

that is very soft to the touch; that of *O. nitidus* is shorter (up to 12 mm) but similar in texture. Underparts of head and body are bright, whitish gray. Dorsal surfaces of feet are unpigmented and covered with short white hairs. Tails are generally sharply bicolored: brown along their dorsal surfaces and unpigmented along most of the ventral side. Our visual impression of both species is that of moderately large rats with white feet, bicolored tails, lustrous reddish or tawny brown dorsal coat—which is especially long and soft in *O. macconnelli*—and whitish gray ventral pelage.

Oryzomys yunganus has white front and hind feet (‘‘hands and feet silvery white above,’’ in Thomas’s description of the holotype) and resembles *O. nitidus* and *O. macconnelli* in this chromatic trait. Upperparts of head and body, however, are dark brown (even darker in some specimens, a slaty brown) and only slightly brighter along the

TABLE 7
Occurrence of Hypothenar Pad among Samples of *Oryzomys yunganus*
(See fig. 17.)

Region (number keys to locality in gazetteer for *O. yunganus*)	N	Presence (and size)[a]		
		Both feet	One foot only	Absent
FRENCH GUIANA (1–3)	18	7 (vs–lg)	1 (vs)	10
SURINAM (6, 8–10)	15	13 (vs–lg)	—	2
GUYANA (12, 13)	10	10 (sm–lg)	—	—
VENEZUELA (14–17)	34	34 (vs–lg)	—	—
COLOMBIA (18a)	1	1 (lg)	—	—
ECUADOR (23, 24, 30, 31)	15	15 (sm–lg)	—	—
PERÚ (32–39, 42–44, 46–48, 50, 52–54)	62	61 (vs–lg)	—	1
BOLIVIA (55–59, 60)	10	8 (sm–lg)	—	2
WESTERN BRAZIL				
Sena Madureira (61)	1	1 (lg)	—	—
Rio Juruá (62, 63–69, 71, 73, 75)	37[b]	30	2	5
Rio Roosevelt (76)	1	1 (lg)	—	—
Rio Saueninä (77)	1	1 (vs)	—	—
CENTRAL BRAZIL				
Serra do Roncador (78)	30	29 (sm–lg)	—	1
NORTHEASTERN BRAZIL				
Pará (79, 80)	5	5 (vs–lg)	—	—
Amapá (81, 82)[c]	4	1 (vs)	—	3

[a] The hypothenar pad is either round or slightly elliptical but may vary in size. The range we noted in most samples extends from a large conspicuous mound (lg) through tubercles of smaller but moderate size to a much smaller but still evident bump (sm). A very small area of concentric ridges (vs), either slightly or not at all raised above the epidermis, forms the most inconspicuous evidence of a pad.

[b] J. L. Patton surveyed the plantar surfaces of these specimens (we studied the skulls but not the skins) and wrote to us that "in none of the specimens is the hypothenar pad well developed."

[c] We actually examined 51 specimens from Amapá but only four are represented by skins and skulls, the rest are skulls only. The reliability of such a small sample has to be checked by much larger series of skins or specimens preserved in fluid.

sides ("dark fulvous, finely and profusely lined with black . . . sides and rump clearer and stronger rufous . . . forehead greyish, lined with black . . . base of whiskers brown, continuous with a dark ring round eyes," in Thomas's view). A wide and dark ring around each eye is typical in examples of *O. yunganus* but is absent from specimens of *O. nitidus* and *O. macconnelli* (eyelids of these two species are dark brown, but not the surrounding fur, which is pigmented like the rest of the head and the body). The dorsal coat is not as thick (7–10 mm over the back and rump; "fur close and glossy, about 9 millim. long on the back," in Thomas's words). Underparts are much darker—a dark grayish white (which Thomas described as "soiled whitish, the bases of the hairs slaty, their tips dull white"). Dorsal surface of the tail is brown, the ventral surface partially pigmented ("whitish below proximally, the remainder greyish brown," as Thomas wrote) or mottled pale brown and not distinctly bicolored in most specimens; however, the range of variation we observed within any large sample includes a few specimens with sharply bicolored tails similar to *O. nitidus* and *O. macconnelli* at one extreme, and some animals with brown, monocolored tails at the other. A medium-sized rat with short fur of somber hues is our visual perception of *O. yunganus,* which contrasts sharply with the

TABLE 8

Descriptive Statistics for Measurements (mm) of *Oryzomys macconnelli, Oryzomys yunganus*, and *Oryzomys megacephalus* from Auyán Tepuy, Venezuela (Locality 14 in gazetteer for *O. yunganus*)

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. Each sample ranges in age from young to old adults. Specimens are identified in the footnotes. *P* is the level of probability derived from a table of cumulative Student's *t* distribution; values less than 0.05 [in boldface] are considered significant to reject the hypothesis that means of any two samples were drawn from the same population.)

	O. macconnelli[a]	*P*	*O. yunganus*[b]	*P*	*O. megacephalus*[c]
LHB	144.9 ± 12.27 (132–166) 12	**<0.001**	126.5 ± 6.61 (115–142) 15	0.4–0.3	120.0 ± 9.89 (99–142) 32
LT	160.1 ± 9.56 (143–175) 12	**<0.001**	116.7 ± 5.79 (107–128) 15	>0.9	116.2 ± 7.57 (90–132) 32
LHF	34.2 ± 1.59 (32–37) 12	**<0.001**	28.3 ± 1.03 (26–30) 15	>0.9	28.2 ± 1.35 (25–32) 32
ONL	34.3 ± 0.62 (33.3–35.2) 12	**<0.001**	31.7 ± 0.81 (30.4–33.2) 13	0.4–0.3	31.1 ± 0.87 (29.8–33.2) 32
ZB	16.9 ± 0.48 (16.0–17.7) 12	**<0.001**	15.8 ± 0.52 (15.0–16.9) 15	0.7–0.6	15.6 ± 0.59 (14.4–16.8) 32
IB	5.4 ± 0.19 (5.1–5.7) 12	0.2–0.1	5.2 ± 0.17 (4.9–5.5) 15	>0.9	5.1 ± 0.17 (4.9–5.5) 32
LR	11.4 ± 0.29 (11.0–11.9) 12	**<0.001**	9.7 ± 0.30 (9.4–10.3) 15	0.8–0.7	9.8 ± 0.46 (8.9–10.8) 32
BR	6.7 ± 0.19 (6.5–7.1) 12	**0.01–0.001**	6.3 ± 0.30 (5.8–6.9) 15	0.4–0.3	6.1 ± 0.32 (5.6–7.0) 32
LB	12.4 ± 0.41 (11.8–13.0) 12	**0.02–0.01**	11.9 ± 0.31 (11.4–12.4) 13	0.5–0.4	11.6 ± 0.37 (10.5–12.4) 32
HBC	8.9 ± 0.27 (8.5–9.5) 12	0.2–0.1	8.7 ± 0.30 (8.2–9.3) 12	0.8–0.7	8.6 ± 0.37 (8.0–9.5) 32
BZP	3.5 ± 0.18 (3.2–3.8) 12	**<0.001**	4.0 ± 0.22 (3.6–4.5) 15	**0.01–0.001**	3.3 ± 0.29 (2.8–4.0) 32
LD	8.7 ± 0.26 (8.3–9.2) 12	**<0.001**	8.0 ± 0.28 (7.6–8.6) 15	0.2–0.1	7.7 ± 0.32 (7.1–8.2) 32
LBP	7.5 ± 0.30 (6.9–7.9) 12	0.5–0.4	7.4 ± 0.33 (7.0–8.3) 15	**<0.001**	6.8 ± 0.27 (6.2–7.5) 32
PPL	11.6 ± 0.43 (10.8–12.2) 12	**<0.001**	10.6 ± 0.41 (10.0–11.2) 13	0.9–0.8	10.7 ± 0.56 (9.9–12.2) 32
LIF	5.2 ± 0.19 (4.9–5.6) 12	**<0.001**	4.7 ± 0.19 (4.3–5.0) 15	0.3–0.2	4.5 ± 0.25 (3.9–4.8) 32
BIF	2.9 ± 0.12 (2.6–3.0)	**<0.001**	2.4 ± 0.10 (2.2–2.5) 15	—	2.4 ± 0.15 (2.0–2.7) 32
CLM1-3	5.1 ± 0.12 (4.8–5.3) 12	—	5.1 ± 0.16 (4.8–5.3) 15	**0.01–0.001**	4.9 ± 0.13 (4.7–5.2) 32
BM1	1.5 ± 0.06 (1.4–1.6) 12	—	1.5 ± 0.05 (1.5–1.6) 15	0.2–0.1	1.4 ± 0.08 (1.3–1.6) 32

[a] AMNH 130880, 130908, 130913, 130928, 130961, 130965, 130970, 130974, 130975, 130983, 131119, 131128.

[b] AMNH 130896, 130898, 130899, 130901, 130905, 130906, 130914, 130916, 130933, 130940, 130955, 130959, 130960, 131125, 131126.

[c] AMNH 130893, 130894, 130897, 130900, 130909, 130910, 103912, 130917, 130919, 130922, 130930, 130938, 130945, 130953, 130954, 130957, 130964, 130966, 130969, 130972, 130973, 130977–130982, 130985, 131021, 131099, 131123, 131134.

TABLE 9

Descriptive Statistics for Measurements (mm) of *Oryzomys macconnelli*, *Oryzomys yunganus*, and *Oryzomys megacephalus* from Quincemil, Perú (Locality 53 in gazetteer for *O. yunganus*)

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. Each sample ranges in age from young to old adults. Specimens are identified in the footnotes. *P* is the level of probability derived from a table of cumulative Student's *t* distribution; values less than 0.05 [in boldface] are considered significant to reject the hypothesis that means of any two samples were drawn from the same population.)

	O. macconnelli[a]	*P*	*O. yunganus*[b]	*P*	*O. megacephalus*[c]
LHB	145.8 ± 9.69 (130–160) 8	**<0.001**	138.2 ± 6.72 (128–149) 9	**0.02–0.01**	130.1 ± 8.95 (119–148) 15
LT	138.6 ± 11.86 (124–157) 7	**<0.001**	113.9 ± 5.80 (108–125) 9	0.4–0.3	111.3 ± 5.81 (102–123) 15
LHF	34.6 ± 1.19 (33–37) 8	**<0.001**	30.9 ± 0.93 (30–32) 9	0.2–0.1	30.3 ± 1.05 (28–32) 17
ONL	34.5 ± 0.98 (33.2–36.1) 7	**0.02–0.01**	32.9 ± 1.20 (31.3–35.3) 9	0.8–0.7	32.7 ± 1.44 (30.4–35.6) 14
ZB	16.9 ± 0.63 (16.0–17.9) 8	0.5–0.4	16.7 ± 0.47 (16.2–17.6) 9	0.8–0.7	16.6 ± 0.69 (15.8–18.1) 13
IB	5.3 ± 0.18 (5.0–5.6) 8	0.2–0.1	5.2 ± 0.10 (5.0–5.3) 9	0.2–0.1	5.1 ± 0.17 (4.7–5.3) 16
LR	11.3 ± 0.70 (10.4–11.9) 8	**0.01–0.001**	10.3 ± 0.41 (9.6–11.0) 9	0.6–0.5	10.1 ± 0.50 (9.2–11.1) 16
BR	6.4 ± 0.45 (5.8–7.0) 8	0.6–0.5	6.3 ± 0.31 (5.9–6.9) 9	—	6.3 ± 0.49 (5.5–7.5) 16
LB	12.3 ± 0.29 (11.9–12.7) 5	0.8–0.7	12.2 ± 0.56 (11.5–13.2) 9	0.4–0.3	12.0 ± 0.53 (11.4–12.9) 14
HBC	9.3 ± 0.16 (9.1–9.5) 7	**<0.001**	8.5 ± 0.24 (8.3–9.0) 9	**0.01–0.001**	9.1 ± 0.48 (8.4–10.1) 13
BZP	3.6 ± 0.26 (3.1–3.9) 8	0.1–0.05	3.7 ± 0.18 (3.4–4.0) 9	**<0.001**	3.3 ± 0.26 (2.9–3.7) 16
LD	8.9 ± 0.53 (8.3–9.8) 8	**0.01–0.001**	8.1 ± 0.32 (7.6–8.7) 9	0.4–0.3	8.3 ± 0.53 (7.6–9.5) 16
LBP	7.2 ± 0.42 (6.5–7.8) 8	—	7.2 ± 0.39 (6.6–7.8) 9	0.3–0.2	7.4 ± 0.37 (6.9–8.1) 16
PPL	11.1 ± 0.47 (10.6–11.8) 7	**0.01–0.001**	10.7 ± 0.54 (9.8–11.5) 9	0.5–0.4	10.9 ± 0.61 (9.8–12.2) 13
LIF	5.2 ± 0.44 (4.7–6.0) 8	—	5.2 ± 0.25 (4.7–5.6) 9	**<0.001**	4.4 ± 0.25 (4.1–5.0) 16
BIF	2.4 ± 0.23 (2.0–2.6) 8	0.4–0.3	2.3 ± 0.21 (1.9–2.7) 9	0.2–0.1	2.4 ± 0.14 (2.1–2.6) 16
CLM1-3	5.1 ± 0.23 (4.9–5.6) 8	—	5.1 ± 0.18 (4.8–5.5) 9	—	5.1 ± 0.22 (4.7–5.5) 16
BM1	1.5 ± 0.09 (1.3–1.6) 8	—	1.5 ± 0.03 (1.5–1.6) 9	**0.01–0.001**	1.4 ± 0.08 (1.3–1.6) 16

[a] FMNH 75268, 75271, 75274–75279.

[b] FMNH 75253, 75254, 75257, 75259, 75261–75264, 75272.

[c] FMNH 75222, 75247-75251, 75255, 75256, 75258, 75260, 75265–75267, 75269, 75270, 75273.

Fig. 18. Dorsal views of crania contrasting adult *Oryzomys megacephalus* (left, MNFS 420) with adult *O. yunganus* (right, MNFS 349). Both specimens were collected at Penedo, right bank of Rio Juruá, Estado do Amazonas, Brazil (locality 68 in gazetteer for *O. yunganus*). ×3. Compare the cranium of *O. yunganus* with those of *O. nitidus* and *O. macconnelli* on the opposite page, adults that were also collected along the Rio Juruá. Note the smaller overall size of *O. yunganus* compared with *O. nitidus* and *O. macconnelli*.

colorful russet *O. nitidus* and long furred *O. macconnelli*.

Juvenile pelage differs in tone between the species. The dorsal coat of juvenile *O. yunganus* is dark slaty gray (similar to but even darker than the juvenile fur of *O. megacephalus*), but the upperparts of juvenile *O. nitidus* are brownish gray. Young *O. macconnelli* also have very dark fur similar in color to that of juvenile *O. yunganus*.

Oryzomys yunganus and *O. megacephalus* are chromatically similar. We cannot detect consistent differences in coloration of front and hind feet, head and extent of eye ring, ears, and tail (including the dorsal-ventral pattern of pigmentation). Color and texture of pelage are the only distinguishing features we noted. *Oryzomys yunganus* has, on average, a thicker dorsal coat (hairs are longer; table 6) that looks and feels more velvety. The difference is best appreciated in prime adult pelage. This distinction applies to all samples regardless of their geographic origin; however, there is considerable overlap in hair lengths and some individuals cannot be identified by this single feature.

Upperparts of *O. yunganus* are also more somber in tone, a dark tawny brown; the distal one-fourth or less of each overhair is dark buff, the remainder dark gray. In *O. megacephalus,* the buff band tends to be brighter and wider, one-third to one-half the length of each hair. Typically, *O. yunganus* appears as dark brown with dark tawny highlights, whereas *O. megacephalus* is more tawny brown and brighter. Both species have gray-

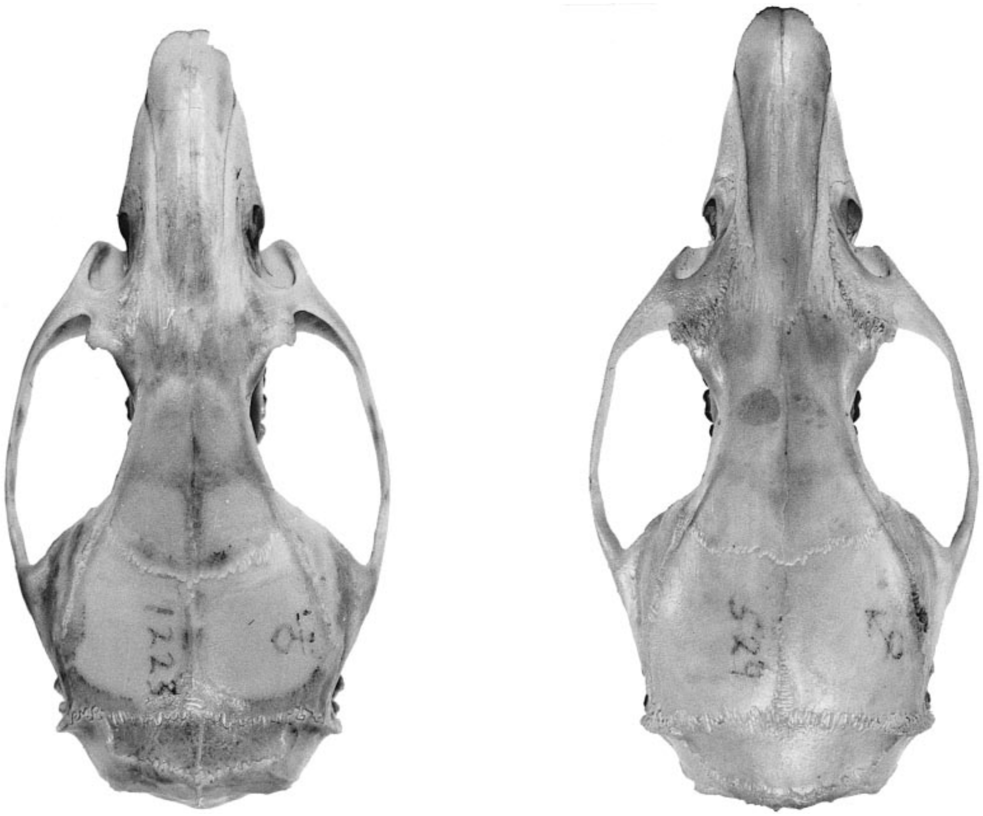

Fig. 19. Dorsal views of adult crania from *Oryzomys nitidus* (left, MNFS 1223) trapped at Igarapé Porongaba, right bank Rio Juruá, Estado do Amazonas, Brazil (locality 63 in the gazetteer for *O. yunganus*), and adult *O. macconnelli* (right, MNFS 529) from Seringal Condor, left bank Rio Juruá (locality 67 in gazetteer for *O. yunganus*). ×3. Compare these views with that of *O. yunganus* on the opposite page.

ish white underparts that are clearly demarcated from the dorsal coat; hairs are gray for their distal half and white to the tips. In any sample of both species from the same place, *O. yunganus* tends to have slightly darker venters (unpigmented bands are narrower), but the overlap in range of tone between the two species disqualifies this chromatic feature as an unambiguous distinguishing trait.

We could not detect differences in lengths of superciliary, genal, and mystacial vibrissae between the species. Like *O. megacephalus,* these sets of vibrissae nearly reach tips of the ears when laid against the stuffed skin or body preserved in fluid, but do not extend beyond them.

PLANTAR PADS: Specimens of *O. nitidus, O. macconnelli,* and nearly all *O. megacephalus* we examined have four interdigital pads on the hind foot, a thenar, and a hypothenar pad; most specimens of *O. yunganus* also have this full complement, but some individuals lack the hypothenar (fig. 17). Among the samples of *O. yunganus* surveyed, the highest frequency of specimens without hypothenar pads occurs in samples from Bolivia, French Guiana, and Estado do Amapá, Brazil (table 7). Presence or absence of a hypothenar is helpful in distinguishing some examples of *O. yunganus* and the morphologically very similar *O. megacephalus* from those geographic regions, but cannot be depended on as an exclusive trait for all specimens in a sample.

CRANIAL SIZE AND PROPORTIONS: Compared with samples of *O. nitidus* and *O. macconnelli*

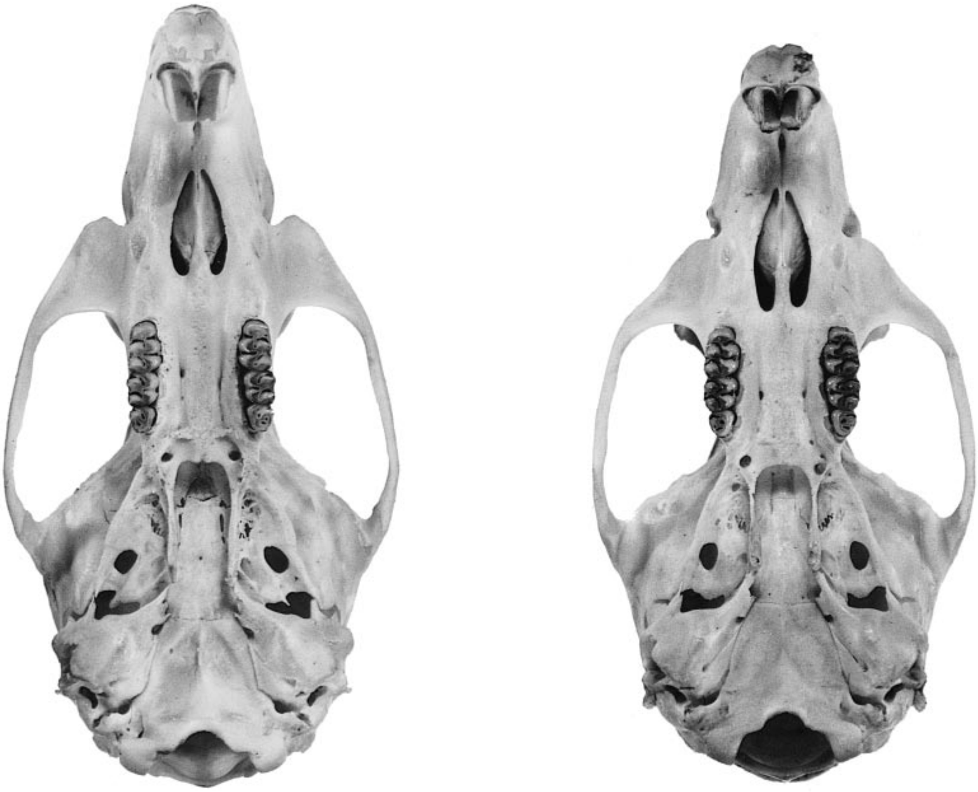

Fig. 20. Ventral views of the same crania of *Oryzomys megacephalus* (**left**) and *O. yunganus* (**right**) shown in figure 18. ×3. Compare the view of *O. yunganus* not only with *O. megacephalus,* but also with those of *O. nitidus* and *O. macconnelli* depicted on the opposite page. The cranium of *O. yunganus* is smaller than that of *O. megacephalus,* but its incisive foramina are longer, both absolutely and relative to occipitonasal length, and its bony palate is longer relative to cranial length, proportions reflected in the ratio diagram (fig. 24).

nelli, crania of *O. yunganus* are smaller, a difference that can be appreciated visually (figs. 18–23) and quantitatively; mean values of most cranial measurements are significantly different between sympatric samples of *O. yunganus* and either *O. nitidus* or *O. macconnelli* (tables 8, 9).

Oryzomys yunganus and *O. megacephalus* closely resemble each other in configuration of the skull and its overall size in some samples, but absolute and proportional differences do exist. As an example of these similarities and differences, we draw on analyses of data from samples of each species collected at Auyán Tepuy, Venezuela. The analyses are presented in the form of descriptive univariate statistics, ratio diagram, and principal components analysis. Comparison of sample means reveals significant differences between the two species in only three measurements: *O. yunganus* has a wider zygomatic plate and a longer bony palate and molar row (table 8).

Crania in the two samples from Venezuela are also proportionally similar with a few exceptions, as is evident in the ratio diagram (fig. 24). Compared with the sample of *O. megacephalus,* the rostrum of *O. yunganus* is shorter relative to occipitonasal length and lengths of diastema, bony palate, and incisive foramina; the zygomatic plate is much wider relative to any other cranial measurement (which reflects the absolute difference between the samples in this feature); the bony palate is longer (also an absolute difference) and postpalatal length shorter relative to oc-

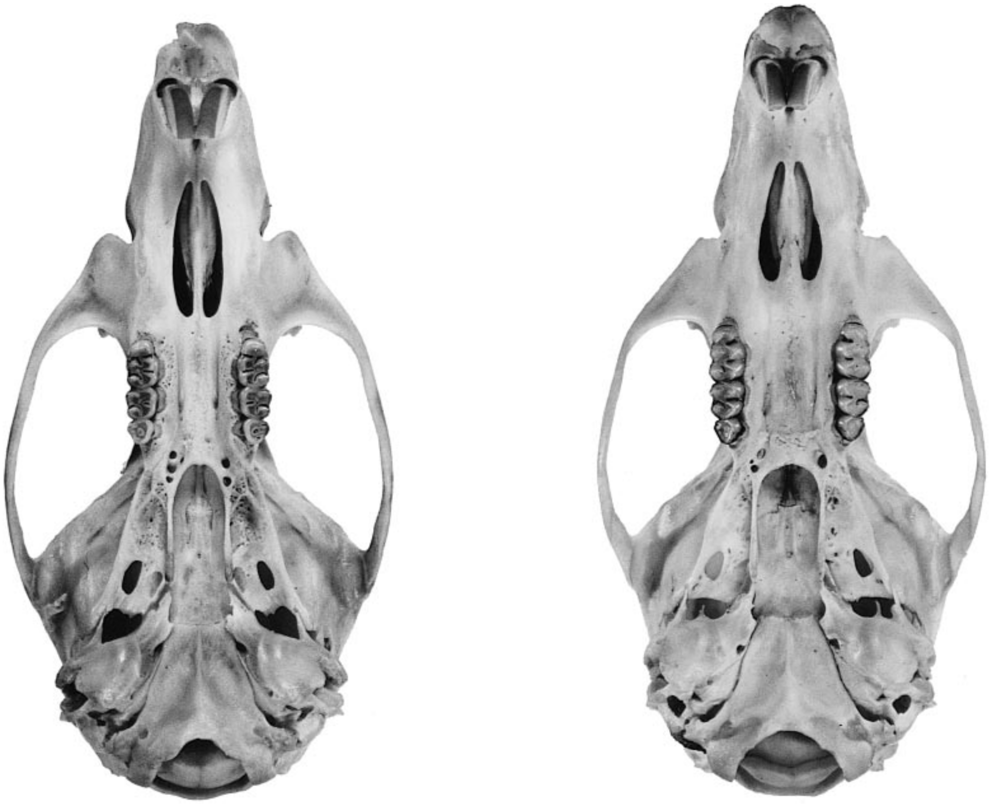

Fig. 21. Ventral views of the same crania of *Oryzomys nitidus* (**left**) and *O. macconnelli* (**right**) illustrated in figure 19. ×3. The long, slitlike incisive foramina of *O. nitidus* and the short, posteriorly diverging incisive foramina of *O. macconnelli* are among the traits distinguishing these two species from *O. yunganus*, which is depicted on the opposite page.

cipitonasal length; incisive foramina are longer relative to their breadth (or narrower relative to their length; ''comparatively narrow incisive foramina'' was a trait of *O. yunganus* that Gardner and Patton (1976: 40) used to distinguish the species from *O. megacephalus*); molar row is shorter relative to length of bony palate, but longer relative to occipitonasal length; and first upper molar is wider relative to length of molar row (we could see this difference when we compared skulls side-by-side, and could also detect it in the univariate statistical analysis; table 8).

Results of principal components analysis (fig. 25; table 10) reveal the degree of dimensional overlap between samples of *O. yunganus* and *O. megacephalus* from Auyán Tepuy and reinforce the proportional contrasts seen in the ratio diagram. The wider (absolutely and relatively) zygomatic plate of *O. yunganus* is mainly responsible for the slightly overlapping clusters along the first axis; differences between the species in breadths of rostrum and first upper molar and lengths of bony palate and incisive foramina also influence, but to a lesser degree, dispersion of scores along that component. There is less distinction between the two species along the second principal component. The dispersion of scores along that axis mostly results from variation in height of braincase, postpalatal length, and breadth of first upper molar.

Thomas (1902), as well as Gardner and Patton (1976), noted that the skull of *O. yunganus* is smaller overall than that of *O. megacephalus*. However, skull size, as estimated by occipitonasal length and zygomatic breadth, does not distinguish our two samples from Auyán Tepuy in either univariate

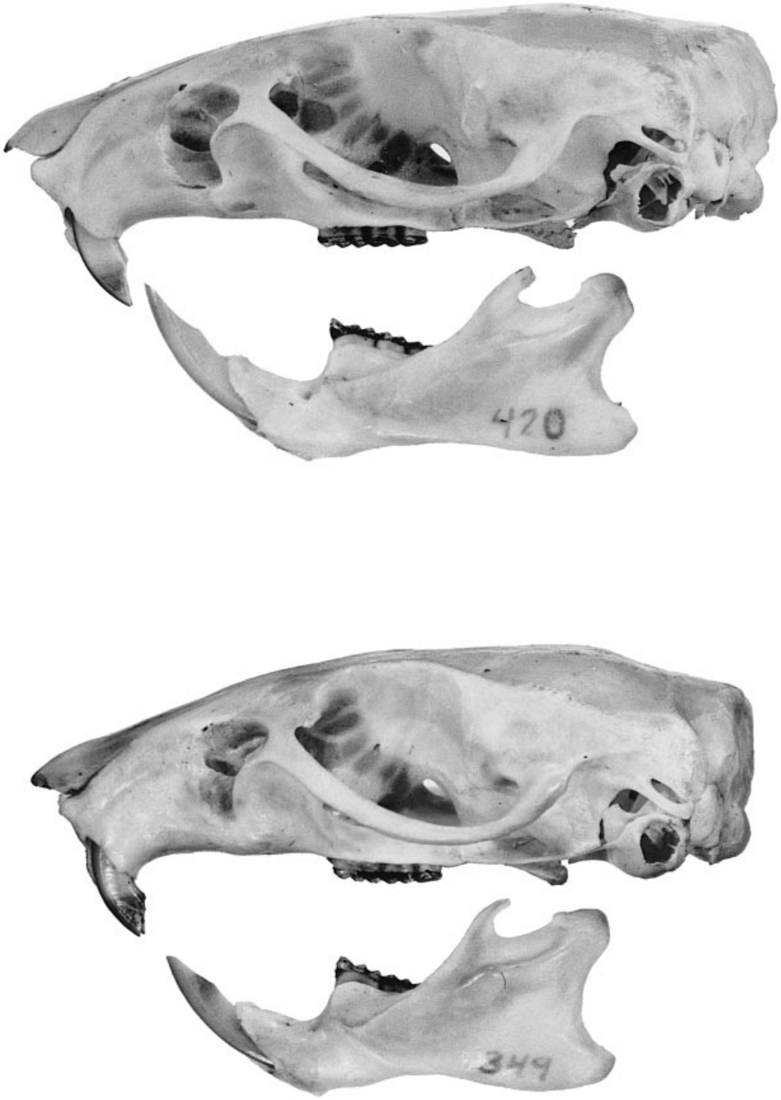

Fig. 22. Lateral views of cranium and dentary from same specimens of *Oryzomys megacephalus* (**top**) and *O. yunganus* (**bottom**) shown in figures 18 and 20. ×3. Zygomatic plates of the two species are about the same width, so the plate of *O. yunganus* is actually wider relative to length of skull (see fig. 24). The posterior margin of the dentary between condyloid and angular processes is more deeply concave in *O. megacephalus* than in *O. yunganus*.

(table 8) or multivariate analyses (table 10). The combination of differences in zygomatic breadth, actual and relative lengths of incisive foramina, bony palate, postpalatal region, and width of first molar provide more useful discrimination.

This suite of features does not distinguish all samples of *O. yunganus* and *O. megacephalus* we examined from throughout their broad distributional ranges in the Guianas and Amazon Basin. Various cranial measurements vary geographically. Discriminating traits significant in one part of the range may be uninformative when applied to samples from other regions. To illustrate this variation, we analyzed additional samples of *O. yunganus* and *O. megacephalus* collected from the same localities in Perú, the Guianas,

Fig. 23. Lateral views of cranium and dentary from same specimens of *Oryzomys nitidus* (**top**) and *O. macconnelli* (**bottom**) portrayed in figures 19 and 21. ×3.

and different regions of Brazil; results are presented in scatter diagrams (figs. 25, 26) representing the projection of specimen scores onto first and second principal components. Univariate descriptive statistics for each species are listed in appendices A and C.

The dispersion of scores reflecting differences between samples of the two species from Quincemil, Perú (fig. 25), is similar to that for samples from Auyán Tepuy in Venezuela. Variation in breadth of rostrum, width of zygomatic plate, postpalatal length, and length of incisive foramina is most important in determining the spread of scores along the first axis (table 10). Dispersion along the second principal component is influenced primarily by variation in breadth of rostrum, height of braincase, and lengths of diastema, bony palate, and incisive foramina. Again,

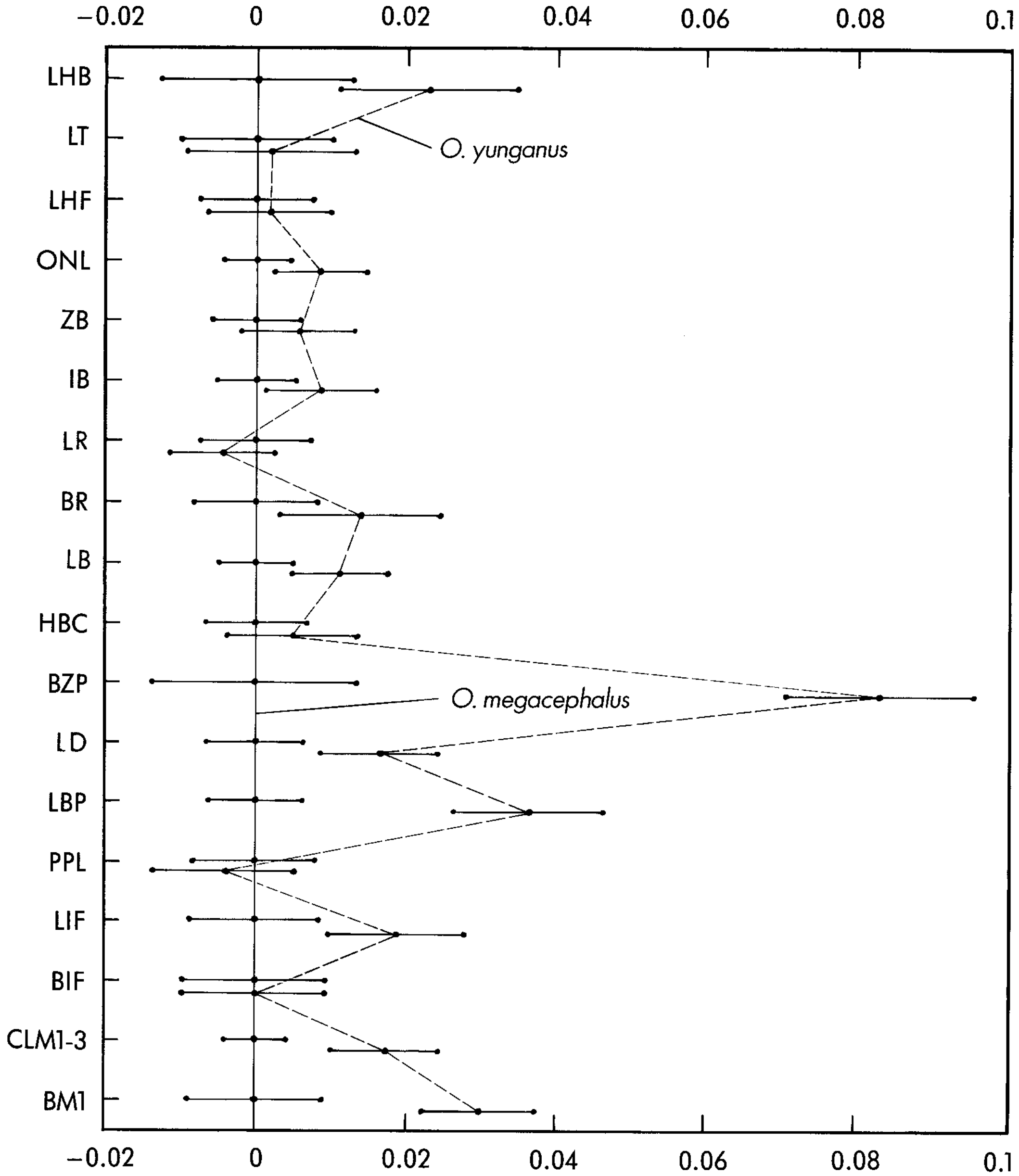

Fig. 24. Ratio diagram illustrating certain proportional relationships between samples of adult *Oryzomys megacephalus* (the standard) and *O. yunganus* from Auyán Tepuy, Venezuela (locality 14 in gazetteer). Data are derived from values for mean, standard deviation, and sample size of variables listed in table 8. The procedure used for generating this diagram is explained in Materials and Methods.

overall size of cranium, as indicated by occipitonasal length and zygomatic breadth, does not distinguish the two species (see descriptive statistics in table 9).

There is no significant separation of scores into clusters along the first principal component in our analyses of samples from Guyana and Surinam, as well as from French Guiana (fig. 25). Variation in length and breadth of rostrum, length of diastema, postpalatal length, and breadth of incisive foramina is primarily responsible for the spread of

TABLE 10

Results of Principal Components Analyses of Adult *Oryzomys yunganus* and *Oryzomys megacephalus* from Venezuela, Perú, Guyana, Surinam, and French Guiana

(Component loadings most strongly influencing dispersion of scores are in boldface. Numbers in parentheses key to localities in gazetteer for *O. yunganus* and on map in fig. 14. See fig. 25.)

	Principal components							
	VENEZUELA Auyán Tepuy (14)		PERÚ Quincemil (53)		GUYANA and SURINAM (10–13)		FRENCH GUIANA (1–3, 5)	
	First	Second	First	Second	First	Second	First	Second
ONL	0.022	0.012	0.032	0.022	0.032	0.004	0.025	0.004
ZB	0.022	0.014	0.027	0.017	0.021	0.003	0.040	0.004
IB	0.012	0.005	0.014	0.002	0.009	0.015	0.019	0.007
LR	0.016	0.022	0.037	0.021	**0.048**	–0.009	0.025	0.011
BR	**0.030**	0.023	**0.044**	**0.042**	**0.049**	0.018	**0.054**	0.013
LB	0.021	0.006	—	—	0.016	0.015	0.025	–0.005
HBC	0.020	**0.026**	0.005	**0.051**	0.002	0.015	0.036	–0.002
BZP	**0.115**	–0.015	**0.074**	–0.011	0.020	**0.053**	**0.058**	**–0.079**
LD	0.029	0.011	0.034	**0.046**	**0.047**	0.012	0.031	–0.000
LBP	**0.032**	–0.014	0.017	**0.047**	0.039	0.021	0.014	–0.006
PPL	0.020	**0.037**	**0.077**	0.003	**0.051**	–0.014	**0.041**	–0.027
LIF	**0.035**	–0.011	**0.076**	**–0.068**	0.016	0.014	0.027	–0.010
BIF	0.005	–0.003	–0.023	0.016	**0.070**	**–0.045**	**0.046**	**0.058**
CLM1–3	0.007	–0.011	0.004	–0.002	0.006	0.003	0.002	–0.005
BM1	**0.025**	**–0.030**	0.024	–0.016	0.005	0.029	–0.016	–0.001
Eigenvalue	0.026	0.007	0.025	0.015	0.018	0.008	0.017	0.011
% Variance	540.7	140.9	400.8	240.5	420.7	180.1	370.8	240.0

scores (table 10). However, there is separation of scores along the second axis in each of those two scatterplots, influenced mainly by breadth of zygomatic plate and incisive foramina. Skulls of *O. yunganus* and *O. megacephalus* from Guyana, Surinam, and French Guiana are closely similar in shape and size, but examples of *O. yunganus* have a wider zygomatic plate and narrower incisive foramina (see descriptive statistics for these measurements in appendices A and C).

Although dimensions of the skull are closely similar in most samples of *O. yunganus* and *O. megacephalus,* they are dissimilar in the samples collected along the Rio Juruá in Acre and western Amazonas, Brazil. We provide results of two analyses: (1) comparison of a sample of each species collected at a single locality, Penedo, on the right bank of the river; (2) comparison of all samples of each species collected at the same localities along both sides of the river in Acre and Amazonas. Differences in occipitonasal length, zygomatic breadth, length and breadth of rostrum, lengths of diastema and bony palate, and postpalatal length are primarily responsible for dispersion of specimen scores of the two species, in the form of overlapping clusters, along the first principal component in each scatterplot (fig. 26; table 11). Dispersion of scores along the second axis is affected mainly by variation in length and breadth of the incisive foramina, and there is no significant clustering of scores representing each species. All these cranial measurements are greater in samples of adult *O. megacephalus* compared to those of *O. yunganus* (contrast means from the samples of each species in appendices A and C). This distinction is also obvious when individuals of the same age of each species are compared visually (figs. 18, 20, 22).

In contrast to samples from the western Amazon Basin of Brazil, crania of the two species are nearly the same size in samples from the eastern Amazon Basin of Brazil (see mean values for occipitonasal length and zygomatic breadth for each species listed in appendices A and C). Occipitonasal length and zygomatic breadth do not significantly

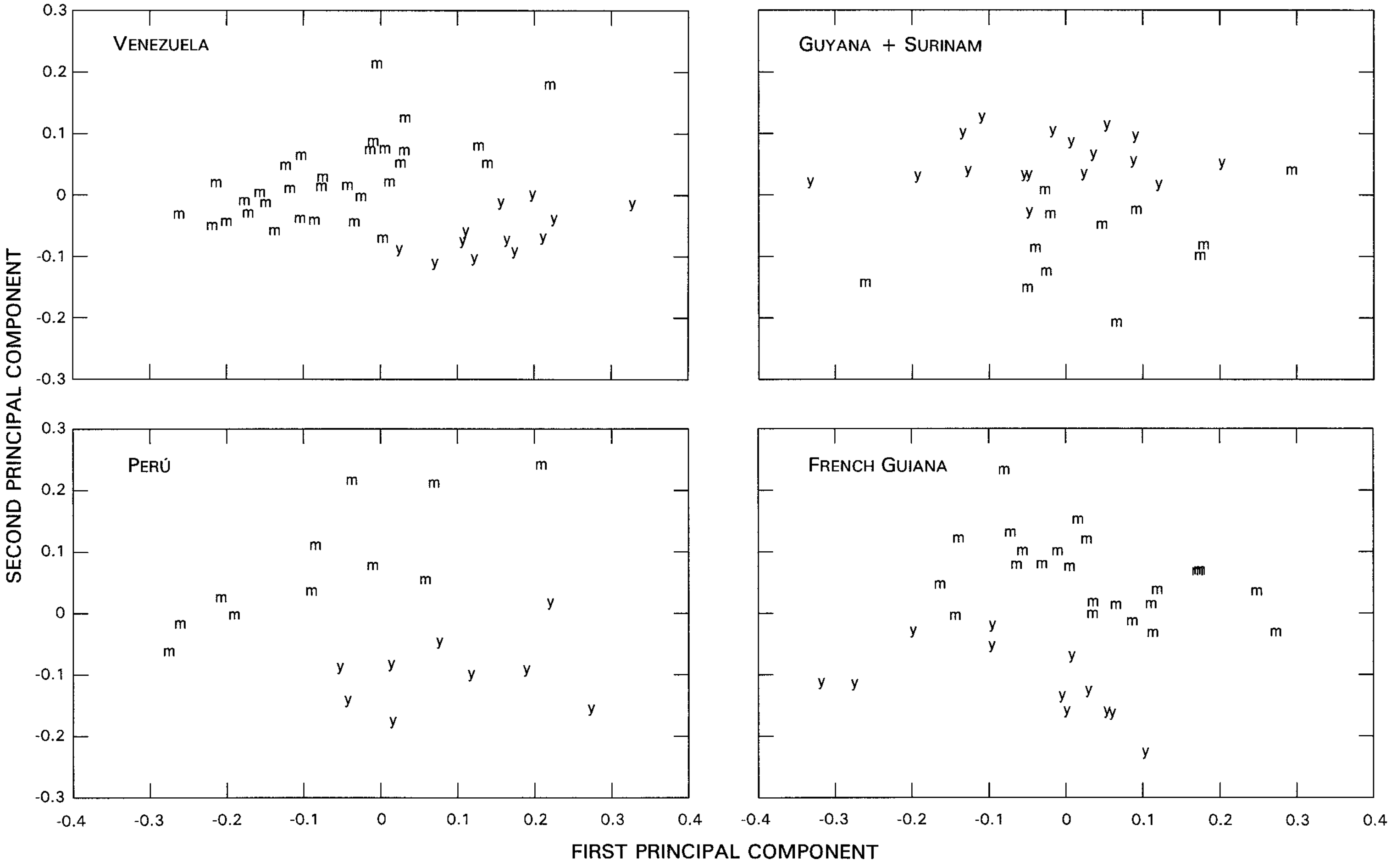

Fig. 25. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 10) and projected onto the first and second principal components extracted from analysis of young to old adult *Oryzomys yunganus* (**y**) and *O. megacephalus* (**m**) from localities of sympatry (see gazetteer for *O. yunganus* and appendix G). Venezuela (Auyán Tepuy, locality 14): *O. yunganus*, *N* = 12; *O. megacephalus*, *N* = 31. Perú (Quincemil, locality 53): *O. yunganus*, *N* = 9; *O. megacephalus*, *N* = 11. Guyana (Kwabanna, locality 12; Santa Cruz, locality 13) and Surinam (Tafelberg, locality 10; Kaiser Gebergte, locality 11): *O. yunganus*, *N* = 17; *O. megacephalus*, *N* = 12. French Guiana (Arataye, locality 1; Paracou, locality 5): *O. yunganus*, *N* = 12; *O. megacephalus*, *N* = 23. Compare with figure 26 and see discussion in text.

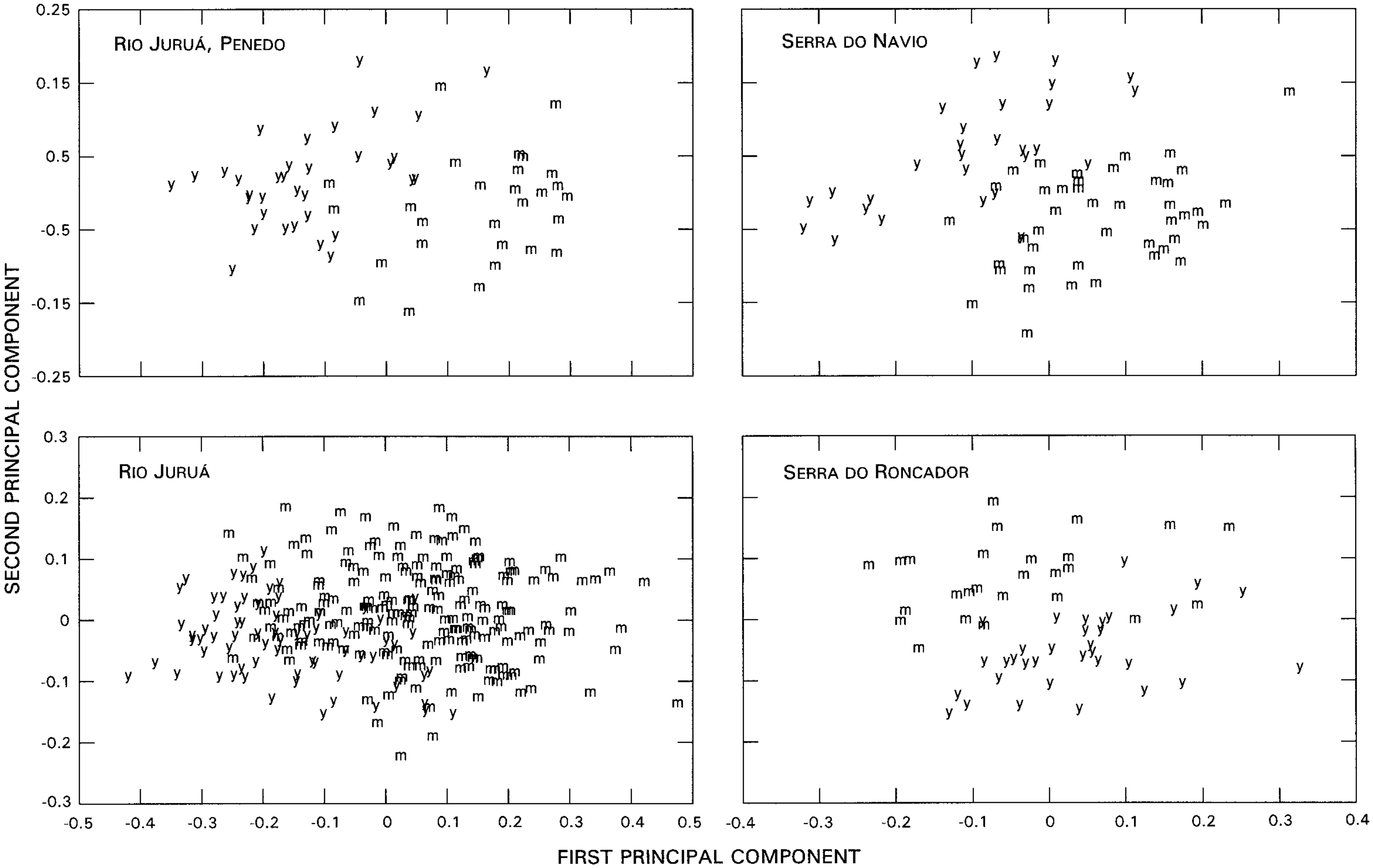

Fig. 26. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 11) and projected onto the first and second principal components, extracted from analysis of young to old adult *Oryzomys yunganus* (**y**) and *O. megacephalus* (**m**) from localities of sympatry (see gazetteer for *O. yunganus* and appendix G) in western Brazil (left two plots) and eastern Brazil (right two plots). Rio Juruá, Penedo (right bank, locality 68): *O. yunganus*, *N* = 34; *O. megacephalus*, *N* = 28. Rio Juruá, all samples (localities 62, 63, 65–71, 73, and 74, right and left banks): *O. yunganus*, *N* = 69; *O. megacephalus*, *N* = 199. Serra do Navio (locality 82): *O. yunganus*, *N* = 29; *O. megacephalus*, *N* = 44. Serra do Roncador (locality 78): *O. yunganus*, *N* = 33; *O. megacephalus*, *N* = 26. Compare with figure 25 and see discussion in text.

TABLE 11

Results of Principal Components Analyses of Adult *Oryzomys yunganus* and *Oryzomys megacephalus* from Western and Eastern Brazil

(Component loadings most strongly influencing dispersion of scores are in boldface. Numbers in parentheses key to localities in gazetteer for *O. yunganus* and on map in fig. 14. See fig. 26.)

	Principal components							
	WESTERN BRAZIL				EASTERN BRAZIL			
	Rio Juruá Penedo (68)		Rio Juruá Acre, Amazonas (62, 63, 65–71, 73, 74)		Amapá Serra do Navio (82)		Mato Grosso Serra do Roncador (78)	
Variable	First	Second	First	Second	First	Second	First	Second
ONL	**0.055**	-0.000	**0.048**	0.003	0.036	0.006	0.022	0.017
ZB	**0.047**	-0.004	**0.044**	-0.001	0.035	0.002	0.019	0.022
IB	0.015	-0.004	0.021	0.007	0.018	-0.011	0.005	0.005
LR	**0.064**	0.001	**0.059**	0.005	**0.054**	-0.000	0.032	0.013
BR	**0.064**	-0.001	**0.067**	0.007	**0.047**	0.021	0.037	0.027
LB	0.035	0.000	0.028	0.000	0.016	0.006	0.020	0.014
HBC	0.030	-0.004	0.035	0.003	0.021	-0.003	0.012	0.005
BZP	0.029	0.030	0.038	-0.015	0.000	**0.054**	**0.055**	-0.018
LD	**0.076**	0.000	**0.068**	0.005	**0.047**	0.015	0.033	0.029
LBP	**0.069**	-0.022	**0.050**	0.031	0.022	0.026	0.023	0.005
PPL	**0.063**	-0.005	**0.059**	0.000	**0.061**	-0.009	0.019	**0.038**
LIF	0.018	**0.059**	0.029	**-0.049**	0.012	0.025	**0.061**	**-0.041**
BIF	0.022	0.006	0.024	**-0.044**	**0.050**	**-0.041**	**0.040**	-0.004
CLM1-3	0.025	0.005	0.014	0.001	0.007	-0.001	0.008	-0.004
BM1	-0.003	0.010	-0.002	-0.011	-0.015	0.007	0.020	-0.034
Eigenvalue	0.033	0.005	0.028	0.006	0.018	0.007	0.015	0.007
% Variance	61.2	9.6	53.8	11.0	41.2	15.7	36.2	18.4

affect the spread of specimen scores along the first principal component (fig. 26; table 11). In the sample from Serra do Navio in Amapá, variation in length and breadth of the rostrum, length of diastema, breadth of incisive foramina, and postpalatal length are more influential. Breadths of rostrum and zygomatic plate are primarily responsible for the position of scores along the second principal component but do not provide significant separation of the clusters. In the sample from Serra do Roncador in Mato Grosso, variation in breadth of zygomatic plate along with length and breadth of incisive foramina mainly determine the scatter of scores along the first principal component but do not distinguish the two species. Better discrimination occurs along the second principal component, with the dispersion of scores being affected mainly by variation in postpalatal length (longer in *O. megacephalus*) and length of incisive foramina (longer in *O. yunganus*).

In summary, we note that overall skull size is not a reliable discriminator between *O. yunganus* and *O. megacephalus* in many regions where they occur together. Instead, the combination of a wider (usually absolutely) zygomatic plate and longer, narrower incisive foramina offers a better criterion for distinguishing *O. yunganus* from *O. megacephalus.* Most specimens can be sorted into one or the other species just by examining these traits of the skulls.

The opposite is true for samples from western Brazil along the Rio Juruá: a combination of length and breadth measurements reflects a much larger skull for *O. megacephalus* as opposed to *O. yunganus,* and overall size is the primary cranial feature that distinguishes the two species in these western samples, a difference that is apparent visually without consulting measurements. Overall cranial size overshadows any absolute difference in breadth of zygomatic plate that may exist between samples of the two species. In

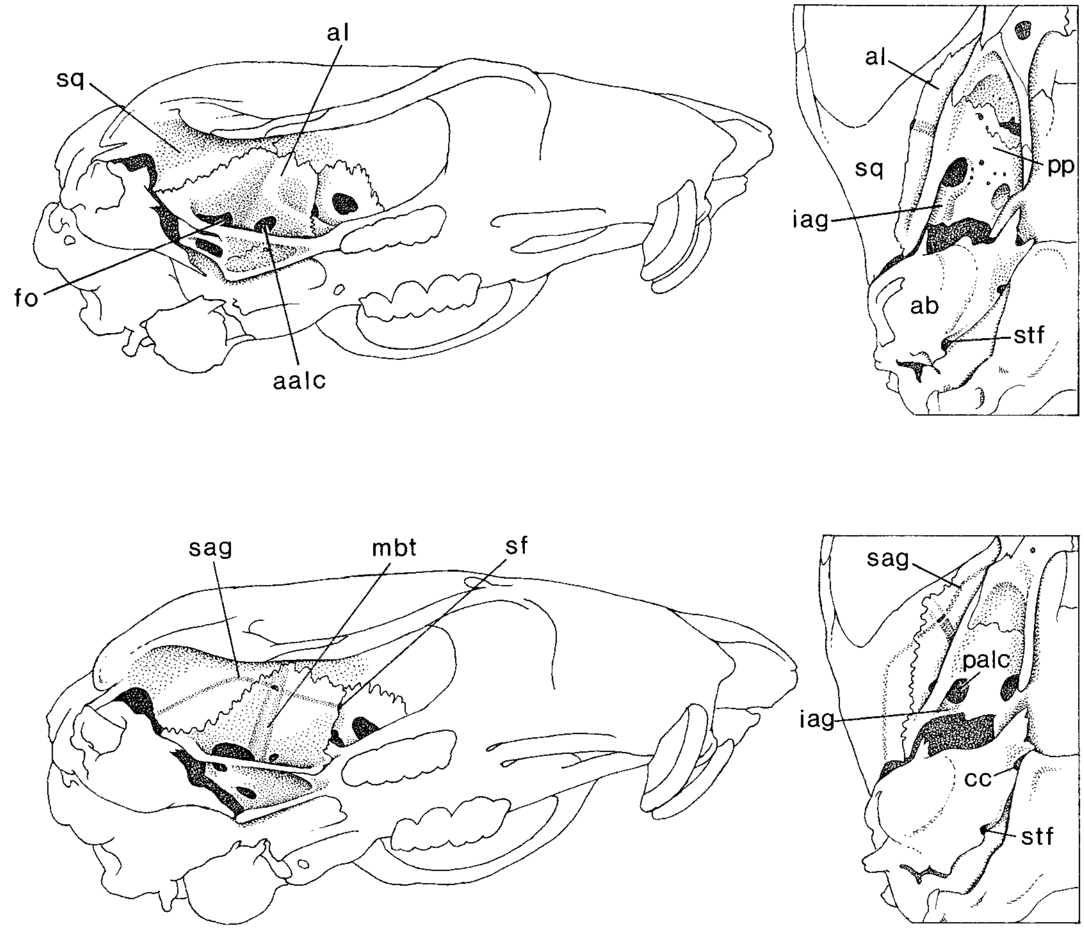

Fig. 27. Contrasts between modified and complete cephalic arterial patterns reflected by bony and foraminal landmarks in the squamosal-alisphenoid region (left drawings) and the ventral surface of the pterygoid plate and auditory bulla (right drawings). *Oryzomys yunganus*, *O. megacephalus*, and *O. laticeps* (**top**; drawn from AMNH 291909, an *O. megacephalus* from Perú) exhibit a modified cephalic arterial circulation: no squamosoalisphenoid groove (**sag**) etches the inner surfaces of the squamosal (**sq**) and alisphenoid (**al**) bones, and no sphenofrontal foramen (**sf**) occurs in the alisphenoid-orbitosphenoid junction (supraorbital branch of stapedial artery absent); however, a large stapedial foramen (**stf**) and prominent groove (**iag**) in the posterolateral corner of the pterygoid plate (**pp**) trace the passage of the stapedial artery and its infraorbital extension, respectively; the latter enters the posterior opening of the alisphenoid canal (**palc**) and abruptly reenters the braincase through the canal's anterior opening (**aalc**). This pattern is like that described and diagramed for *Oligoryzomys* by Carleton and Musser (1989).

Oryzomys nitidus (**bottom**; based on AMNH 211736, Bolivia) and other species in the former *O.* ‘‘*capito*’’ complex have a complete cephalic arterial circulation (table 52) in which the stapedial artery divides into an infraorbital branch and a supraorbital branch that courses in the squamosoalisphenoid groove and enters the orbit through a sphenofrontal foramen. This pattern, likely primitive, is similar to that described and diagramed for *Microryzomys* by Carleton and Musser (1989). Other abbreviations: **ab**, auditory bulla (ectotympanic); **cc**, carotid canal; **fo**, foramen ovale; **mbt**, trough for masticatory-buccinator branch of maxillary nerve.

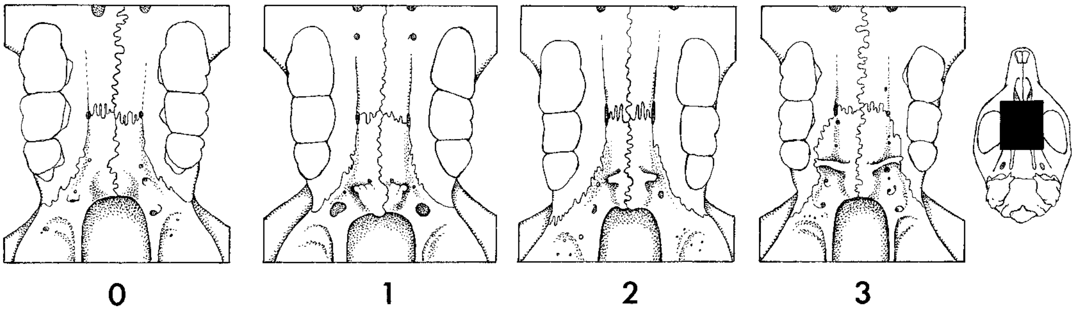

Fig. 28. Variation in expression of bony palatal excrescences. Character states, as exemplified by four adult *Oryzomys megacephalus* from Auyán Tepuy in eastern Venezuela (sample 5 in table 1): From left to right, **O**, AMNH 130967; **1**, AMNH 130899; **2**, AMNH 130954; **3**, AMNH 130969. The four expressions are further defined in table 12.

the principal components analyses for the single sample from Penedo on the Rio Juruá, as well as all Rio Juruá samples combined, breadth of zygomatic plate influenced dispersion of specimen scores only along the third principal component (not illustrated). The plate is relatively wider in *O. yunganus,* but that proportional contrast is not as obvious visually (fig. 22) because mean values for breadth of zygomatic plate from samples of *O. megacephalus* are only slightly greater than sample means for *O. yunganus* (compare descriptive statistics in appendices A and C).

TABLE 12

Variation in Bony Palatal Excrescences in Samples of *Oryzomys yunganus* and *Oryzomys megacephalus* Collected in Three Localities of Sympatry

(Number in parentheses keys to locality listed in gazetteer for *O. yunganus.*)

Country, locality, and species	Expression of excrescences[a] 0	1	2	3
FRENCH GUIANA				
Paracou (5)				
O. yunganus	1	6	3	3
O. megacephalus	3	10	9	10
VENEZUELA				
Auyán Tepuy (14)				
O. yunganus	1	23	4	1
O. megacephalus	3	10	21	14
BRAZIL				
Penedo, Rio Juruá (68)				
O. yunganus	3	32	3	5
O. megacephalus	0	10	9	20

[a] Definition of character-states: **0**, posterior portion of bony palate is either smooth or only slightly thickened and bumpy; **1**, a medial bony mound that may also have slight lateral protuberances; **2**, a medial bony mound with discrete bony projections that extend laterally but not far enough to touch sides of the bony palate; **3**, a medial bony mound with elongate lateral projections that extend far enough to either touch or fuse with sides of the bony palate. The four states are illustrated in figure 28. See text for discussion.

CAROTID CIRCULATORY PATTERN: Specimens of *O. nitidus* and *O. macconnelli* possess the primitive circulatory arrangement of arteries associated with the cephalic blood supply (Bugge, 1970; Carleton, 1980). Conspicuous landmarks of the pattern on the skull are a *squamosoalisphenoid groove,* which is visible through the braincase (often perforating the bone where it crosses the depression for the masticatory–buccinator nerve), leading to a *sphenofrontal foramen* at the junction of the orbitosphenoid, alisphenoid, and frontal; a large *stapedial foramen,* which is located between the otic capsule and periotic bone; and a *posterolateral groove* scoring the ventral surface of the pterygoid plate (fig. 27). To appreciate the overlay of these landmarks with the arterial pattern, see the illustration of the primitive carotid configuration in *Microryzomys* documented by Carleton and Musser (1989).

Oryzomys yunganus and *O. megacephalus* have a modified carotid circulatory pattern (fig. 27), one similar to that described for species of *Oligoryzomys* (Carleton and Musser, 1989). Specimens of each do not have a sphenofrontal foramen and the accompanying squamosoalisphenoid groove, but do possess a large stapedial foramen and a prominent posterolateral groove on the pterygoid plate. Lack of a sphenofrontal foramen and squamosoalisphenoid groove indicates that the supraorbital branch of the stapedial artery is absent. For species in which the supraorbital branch is present, such as *O. nitidus* and *O. macconnelli,* the artery ‘‘passes across the squamosal and alisphenoid bones, scoring the squamosoalisphenoid groove, and emerges at the sphenofrontal foramen’’ (Carleton and Musser, 1989: 35). Retention of a stapedial foramen and posterolateral groove in *O. yunganus* and *O. megacephalus* indicates that the stapedial artery is retained, and its infraorbital branch passes along the groove on the pterygoid plate, enters the posterior end of the alisphenoid canal, and emerges into the orbit through the anterior alar fissure.

PALATAL EXCRESCENCES: These are irregular bony growths on the midventral surface of the palatal bridge near its posterior margin. They may take the form of a simple mound, usually with a rough surface, or a mound from which bony, winglike processes project (fig. 28). Gardner and Patton (1976) referred to these irregular ossifications as ‘‘excrescences’’ and noted that, compared with *O. megacephalus, O. yunganus* has ‘‘a marked tendency for lateral as well as medial development of palatal excrescences’’ (p. 40).

We tested their observation by surveying pairs of species samples from three localities. We picked these samples only because they were readily available; fortunately, the samples contain specimens of each species from different regions of their distributional ranges. Excrescences adorn the bony palate of most specimens of *O. yunganus* and *O. megacephalus.* In each pair of samples, medial bony mounds supporting prominent lateral projections occur more frequently among samples of *O. megacephalus* than *O. yunganus,* just the opposite of published observation (table 12). The variations in form of these palatal calcifications and their frequency distributions within samples of the two species render them unreliable as a distinguishing trait.

MOLAR OCCLUSAL PATTERN: There is little difference in absolute mean values for length of molar row or breadth of first upper molar among samples of *O. nitidus, O. macconnelli, O. yunganus,* and *O. megacephalus* (tables 8, 9, 14). The arrangement of cusps, interconnecting ridges, and valleys between cusps and ridges forms diagnostic occlusal patterns on the second upper and lower molars. Variation in this configuration provides distinctive traits that distinguish examples of *O. nitidus, O. macconnelli,* and *O. yunganus* from specimens of *O. megacephalus.*

In each second upper molar of three of these four species (*O. megacephalus* is the exception), the paraflexus (between paracone and anteroloph) is short (fig. 29A, B). The mesoflexus (between paracone and mesoloph) is interrupted by an enamel partition, creating an enamel-lined pit or fossette (which Gardner and Patton, 1976, as well as Musser and Williams, 1985, described as an ‘‘enamel island’’) between the paracone and protocone. The modified mesoflexus is either a deep or shallow channel between the paracone and mesoloph; the pattern is clearly seen in the slightly worn teeth of nestlings and some juveniles (fig. 29A). As wear proceeds, the posterolabial portion of the paracone fuses with the anterolabial margin of the mesoloph, the mesoflexus channel is closed, and another fossette is formed labial to the medial fossette (fig. 29B). Most specimens of these three species have the occlusal surface configuration described above; its key elements are a *short paraflexus and two fossettes or ‘‘enamel islands’’* (fig. 30). The pattern is common to many species of *Oryzomys* (*O. alfaroi,* for example; fig. 63).

The pattern characteristic of *O. yunganus* may be obliterated on excessively worn molars of old adults. It can still be detected, however, in animals with molars worn to the stage where coronal patterns have almost disappeared. In such teeth, the labial fossette is obliterated but the medial fossette is indicated by a low enamel mound set in a smooth basin; some indication of a short paraflexus is also usually present (fig. 33).

Second upper molars of *O. megacephalus* lack a medial fossette (figs. 29C, 30D). The paracone is separated from the anteroloph by a long paraflexus, and from the mesoloph by a single small fossette, which presumably is

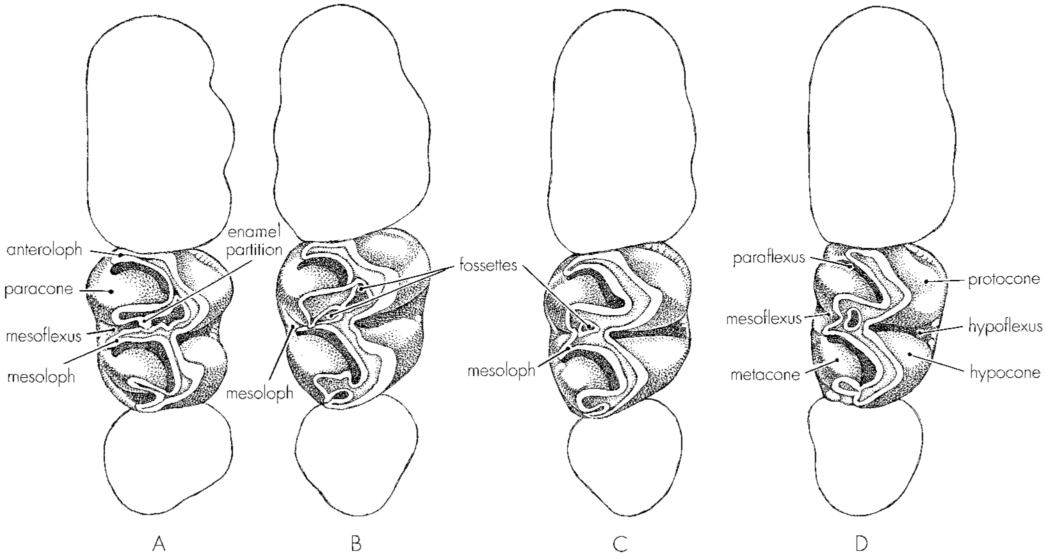

Fig. 29. Occlusal patterns of second upper molars in three species of *Oryzomys*. **A**, Juvenile *O. yunganus* (AMNH 266532); **B**, adult *O. yunganus* (AMNH 231666); **C**, young adult *O. megacephalus* (AMNH 231655); **D**, juvenile *O. talamancae*. Terminology is that proposed by Reig (1977). Depicted is the pattern (**A** and **B**) found in *O. yunganus*, *O. nitidus*, and *O. macconnelli* as contrasted to the configuration (**C** and **D**) typical of *O. megacephalus*, *O. talamancae*, and *O. bolivaris*. See figure 30 on opposite page and discussion in text.

the proximal remnant of the mesoflexus. A *long paraflexus and single fossette,* labial in position, are the key elements distinguishing the second upper molars of *O. megacephalus* from those in the other three species. The *megacephalus* pattern is also characteristic of its trans-Andean congeners, *O. bolivaris* and *O. talamancae* (fig. 63).

Occlusal patterns of second lower molars also sort the four species into two groups. In each second lower molar of *O. nitidus, O. macconnelli,* and *O. yunganus,* a hypoflexid extends lingually halfway across the molar between the protoconid and hypoconid and is separated from a lingual fossettid by the median murid, which has essentially an anterior–posterior orientation (figs. 31A, B, 32). The fossettid is formed when lingual margins of the mesolophid and entoconid coalesce to separate the entoflexid (between mesolophid and entoconid) into a fossettid and lingual crease. Diagnostic elements in this pattern are the *short hypoflexid separated from a fossettid by the median murid.*

In the second lower molar of *O. megacephalus,* a long hypoflexid separates the protoconid and median murid from the hypoconid and medial portion of the entoconid (fig. 31C). The median murid is nearly horizontal or diagonal in position relative to the protoconid. Slightly worn molars of some juveniles demonstrate a pattern in which the anterior half of the molar (metaconid, protoconid, and mesolophid) is separated from the posterior half (entoconid and hypoconid) by a trough extending from lingual to labial side; the depression is present because the mesolophid and anterolingual surface of the entoconid do not touch. The occlusal surface eventually wears to the level where mesolophid and entoconid are fused, thus forming a partition that separates the trough into a shallow entoflexid and long hypoflexid (fig. 31C). A *long hypoflexid extending across most of the molar, diagonal median murid, and lack of fossettid* are the diagnostic traits of the *megacephalus* pattern (fig. 32).

MANDIBLE: General conformation of each dentary is similar among *O. nitidus, O. macconnelli, O. megacephalus,* and *O. yunganus* (figs. 22, 23). Dentaries of *O. yunganus* are smaller than those of *O. nitidus, O. maccon-*

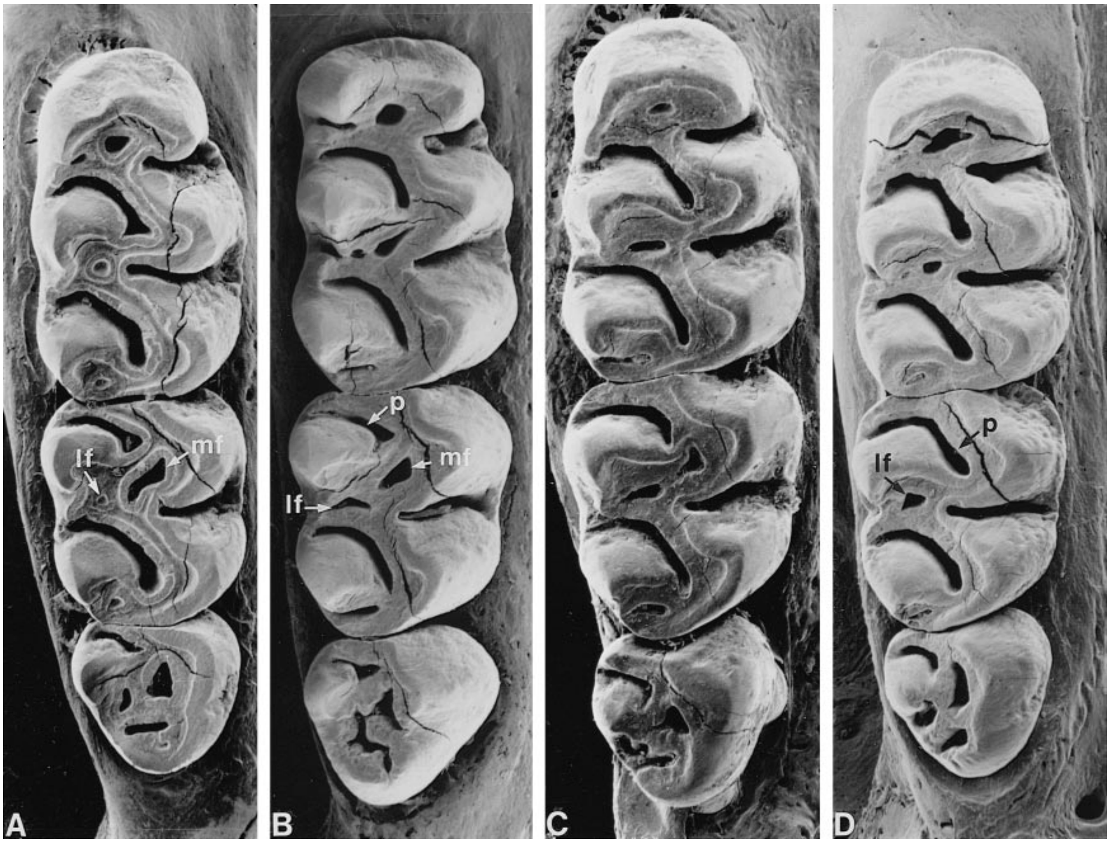

Fig. 30. Occlusal views of right upper molar rows from species of *Oryzomys*. **A**, *O. nitidus*, Bolivia (AMNH 211742; CLM1–3 = 4.8 mm); **B**, *O. macconnelli*, Venezuela (AMNH 131121; CLM1–3 = 5.2 mm); **C**, *O. yunganus*, Perú (AMNH 231666; CLM1—3 = 5.0mm); **D**, *O. megacephalus*, Perú (AMNH 231655; CLM1—3 = 5.0 mm). Labial (**lf**) and medial (**mf**) fossettes along with a short paraflexus (**p**) are common to the second molars of *O. nitidus*, *O. macconnelli*, and *O. yunganus*; a medial fossette is not present in *O. megacephalus* and the paraflexus is long.

nelli, and some samples of *O. megacephalus*. The only other difference noted is the variation in shape of the posterior margin of the dentary between condylar and angular processes. The rim is shallowly concave in *O. yunganus* but more deeply concave in the other three species. Although not an absolute distinction between *O. yunganus* and *O. megacephalus*, the difference is helpful when used in combination with other features to separate specimens of the two species.

CHROMOSOMES: Gardner and Patton (1976) discovered impressive variation in chromosomal traits among their Peruvian samples of what Hershkovitz (1960, 1966) had stated was *O.* ‘‘*capito*.’’ Matching distinctive elements of this variation with unambiguous diagnostic morphological characters allowed them to recognize four species: ‘‘Our determinations are based upon direct comparisons of specimens of known karyotype with most of the holotypes that have been available to us’’ (p. 39). An ‘‘enamel island’’ on each second upper molar and ‘‘comparatively narrow incisive foramina’’ characterized samples with two karyotypic variants that Gardner and Patton identified as *O. yunganus*. They recorded a 2*n* of 58 and FN of 62 for three specimens and a 2*n* of 60 and FN of 66 for two others; the karyotypes are closely similar except for the lack of a small metacentric pair in the former (table 13). This combination of morphology and karyotypes contrasted with specimens that lacked the is-

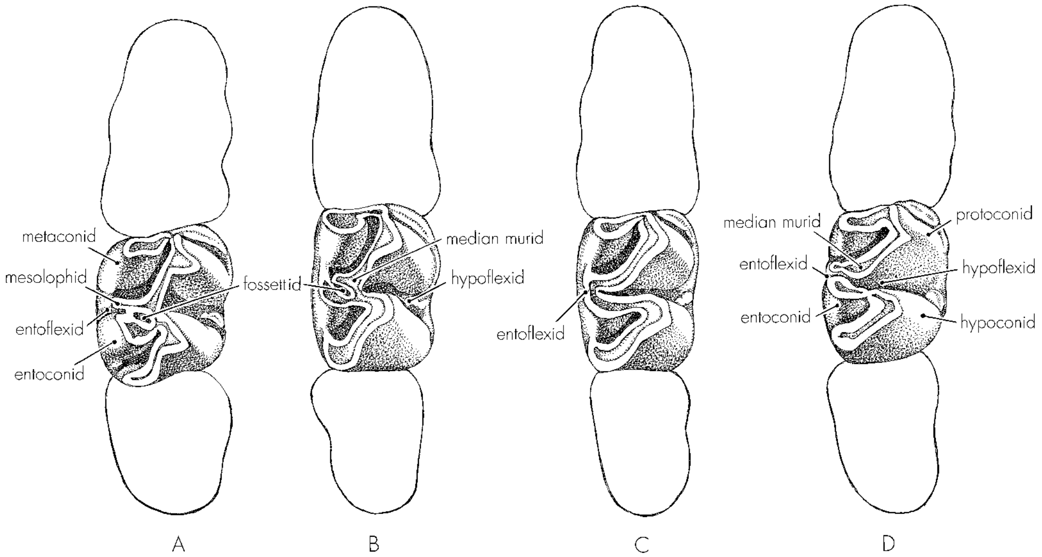

Fig. 31. Occlusal patterns of second lower molars in the same specimens of *Oryzomys yunganus, O. megacephalus,* and *O. talamancae* illustrated in figure 29. Compare with figure 32 on opposite page and see discussion in text.

land, had incisive foramina ''comparatively short, broad, and teardrop-shaped,'' and had a 2*n* of 52 and FN of 62, which they determined to be *O. megacephalus.*

The chromosomal complement of *O. yunganus* is also different from Peruvian samples in which ''enamel islands'' are present in the second upper molars. Gardner and Patton matched one group possessing 2*n* of 80 and FN of 86 with morphology of *O. nitidus,* and another sample with a 2*n* and FN of 64 with the external, cranial, and dental characteristics of *O. macconnelli* (table 13).

Chromosomal distinctions between *O. yunganus* and *O. megacephalus* are also evident in samples from Surinam, the only other region east of the Andes where chromosomal variation among samples of the *O. megacephalus* complex has been reported (Koop et al., 1983; Kerridge and Baker, 1990). Surinam samples of *O. yunganus,* unlike those from Perú, show a greater magnitude of autosomal polymorphism, which is reflected in the range of diploid numbers, 52–59, and fundamental numbers, 64–67 (table 13). Such variation suggests the presence of more than one species, but morphological traits of all these specimens (listed in the gazetteer for *O. yunganus*) are clearly characteristic of *O. yunganus*; that the chromosomal variation occurs within a single species is also indicated by study of allozymic variation (Kerridge and Baker, 1990). Specimens of *O. megacephalus* from Surinam, on the other hand, do not exhibit such polymorphism (''chromosomally monomorphic'' Kerridge and Baker, 1990: 5) and are characterized by a 2*n* of 54 and FN of 58–59.

SYMPATRY: Analyses of morphological and chromosomal variation were used by Gardner and Patton (1976) to separate their samples of the ''*capito*-complex'' into four groups, each of which they characterized as a species. One other component of the study impressively reinforced their definitions. All four morphologies, each corresponding to a distinctive chromosomal complement, were represented by specimens collected by Gardner and Patton themselves at a single locality, Balta, on the Río Curanja in Perú (locality 49 in the gazetteer for *O. yunganus*). Descriptive statistics for samples of all four species are listed in table 14. Among our records, that co-occurrence of *O. macconnelli, O. megacephalus, O. nitidus,* and *O. yunganus* is unique.

In addition to Balta, samples collected from 48 other localities yielded different

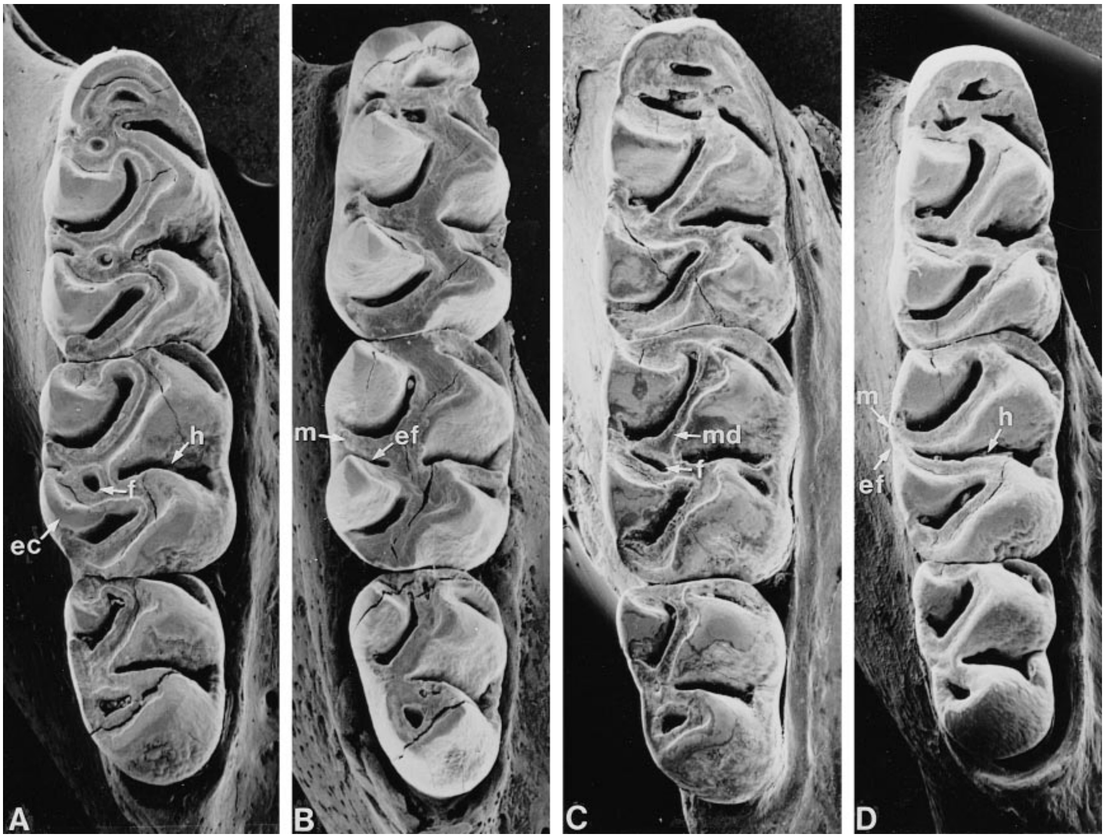

Fig. 32. Occlusal views of right lower molar rows of the same species and specimens of *Oryzomys* that are illustrated in figure 30. **A**, *O. nitidus* (clm1–3 = 5.0 mm); **B**, *O. macconnelli* (clm1–3 = 5.5 mm); **C**, *O. yunganus* (clm1–3 = 5.3 mm); **D**, *O. megacephalus* (clm1–3 = 5.4 mm). The second molar of *O. megacephalus* is nearly bisected by an elongate hypoflexid (**h**) that separates the median murid (**md**) and mesolophid (**m**) from the entoconid (**ec**). The entoflexid (**ef**) is a crease on the lingual surface of the tooth. In the other three species, the hypoflexid extends only halfway across the second molar. Opposite the hypoflexid is a deep entoflexid (**B**) that in some specimens is closed by coalescence of labial margins of mesolophid and entoconid; the result is a enamel-lined pit or fossettid (**f** in **A** and **C**).

combinations of sympatric associations (documented in appendix G). Specimens of *O. megacephalus* were obtained along with *O. yunganus* in all but four of the collection localities, with *O. macconnelli* at 14 sites and with *O. nitidus* at 8. Our resolution of ecological co-occurrence is coarse. We can determine only that specimens of the different species have been taken at the same place (identified by names on specimen labels, in field notes, or museum catalogs), sometimes by the same collector or field team, usually at the same altitude, and roughly within the same time frame. Generally, we do not know if examples of each species were taken in the same trapline or exactly where they were caught in relation to each other at a given site.

The geographic distribution of *O. megacephalus* is broadly concordant with that of *O. yunganus*, although *O. megacephalus* has been collected north of the Río Orinoco in forests of northeastern Venezuela and Trinidad whereas *O. yunganus* has not. It is not surprising, therefore, that *O. megacephalus* occurs together with *O. yunganus* throughout most of its geographic range (see map in fig. 14 as well as appendix G). The ecological interplay between the two species at any site of co-occurrence is unknown to us. Examples

TABLE 13
Summary of Karyotypic Data from Samples of Ten Species of *Oryzomys*[a]

		Pairs of autosomes			Sex			
Species	2*n*	M-SM[b]	ST	A	X	Y	FN	Reference
O. megacephalus								
ECUADOR: Napo[c]	52	6	0	19	T	T	62	Unpubl. data from A. L. Gardner
PERÚ: Junín,								
Ayacucho, Ucayali	52	6	0	19	T	T	62	Gardner and Patton, 1976
Loreto, Ucayali[d]	52	?	?	?	T	T	64	Malygin, 1994
BRAZIL: Acre,								
Amazonas (Rio Juruá)[e]	52	6	0	19	T	T	62	Patton, personal commun.
Amazonas (Manaus area)[f]	54	5	0	21	T	T	62	Silva, 1994; USNM 554848
Pará	54	5	0	21	T	T	62	Present report, fig. 11
Goiás	54	5	0	21	T	T	62	Svartman and Almeida, 1992
VENEZUELA:								
Bolívar	54	5	1	20	T	T	62	Perez-Zapata et al., 1986
Sucre[g]	54	5	1	20	T	T	62	Gardner, personal commun.
SURINAM:								
Sipaliwini[h]	54		(see text)				58–59	Kerridge and Baker, 1990
PARAGUAY:								
Canendiyu	54	5	0	21	T	T	62	Present report, fig. 11
O. laticeps								
BRAZIL:								
Paraíba[i]	52	5	0	21	T	T	62	Svartman and Almeida, 1992
Pernambuco	52	6	0	19	T	T	62	Maia, 1990
O. yunganus								
PERÚ:								
Ayacucho	60	4	0	25	T	T	66	Gardner and Patton, 1976
Ucayali	58	3	0	25	T	T	62	Gardner and Patton, 1976
BRAZIL: Acre,								
Amazonas (Rio Juruá)[e]	58	3	0	25	T	T	62	Patton, personal commun.
SURINAM: Sipaliwini[j]	52–59		(see text)				64–67	Kerridge and Baker, 1990
O. bolivaris								
COSTA RICA[k]	58	9	1	16	ST	T	80	Gardner and Patton, 1976
O. talamancae								
VENEZUELA:								
Aragua	34	13	3	0	T	ST	64	Perez-Zapata et al., 1986
Yaracuy	34	13	3	0	T	ST	64	Present report, fig. 68
Zulia	40–42		(see text)				66–67	Present report, fig. 69
ECUADOR:								
N Gulf Guayaquil	36	11	2	4	T	ST	60	Present report, fig. 70
S Gulf Guayaquil	54	4	0	22	ST	T	60	Present report, fig. 70
O. alfaroi								
MÉXICO: Veracruz	60	23	0	6	T	T	104	Haiduk et al., 1979
ECUADOR	62	16	4	10	ST	T	100	Present report, fig. 71
O. nitidus								
PERÚ: Ayacucho, Ucayali	80	4	0	35	ST	T	86	Gardner and Patton, 1976

TABLE 13
(*Continued*)

Species	2*n*	Pairs of autosomes			Sex		FN	Reference
		M-SM[b]	ST	A	X	Y		
O. emmonsae								
BRAZIL: Pará	80	4	0	35	ST	T	86	Present report, fig. 109
O. macconnelli								
PERÚ: Ucayali[l]	64	1	0	31	T	T	64	Gardner and Patton, 1976
BRAZIL: Amazonas	64	4	0	27	ST	T	70	Present report, fig. 105
VENEZUELA: Bolívar	76	(see text)			ST	T	85	Present report, fig. 105
O. russatus								
BRAZIL: São Paulo[m]	80	4	0	35	ST	T	86	Silva, 1994

[a] **Metacentric** (M), biarmed chromosomes with arms of nearly equal length; **submetacentric** (**SM**), biarmed chromosomes with a short arm at least one-third the length of the other; **subtelocentric** (**ST**), biarmed chromosomes with a short arm less than one-third the length of the other; **acrocentric** (**A**; or **telocentric**), chromosomes with a very minute second arm or no such discernable segment (see the definitions in Patton, 1967). Fundamental Number (**FN**) is derived only from the number of autosomal arms.

[b] Observed or reported as metacentrics only, metacentrics and submetacentrics, or simply biarmed.

[c] Counts are from spreads made by Gardner from USNM 513542, 528353, and 528355, all collected at Limóncocha (sample 10 in table 1); karyotype is identical to that reported by Gardner and Patton (1976) for *O. "capito."*

[d] Sample is from Iquitos and Pucallpa "represented by 17 specimens," which were "found to have two chromosome forms, differing in the size of the 7-th pair of autosomes and X-chromosomes" (Malygin, 1994:103).

[e] Unpublished data provided by J. L. Patton; he and his colleagues karyotyped 20 specimens of *O. yunganus* and 65 examples of *O. megacephalus* collected from various localities along the Rio Juruá in the states of Acre and Amazonas, western Brazil.

[f] Karyotypes are from specimens captured near Manaus (Silva, 1994) and from 80 km north of Manaus (USNM 554848, female; data are from A. L. Gardner).

[g] Derived by A. L. Gardner from chromosomal spreads generously provided by R. S. Voss. Data are from MHNLS 8141 and AMNH 257235 collected in Venezuela, Estado de Sucre, Finca Vuelta Larga, 9.7 km (by road) SE Guaraúnos, 10°33'N/63°07'W (from Voss, 1991:14), 10 m.

[h] Derived from two specimens that were "chromosomally monomorphic," containing no karyotypic "centric fusion polymorphisms" (Kerridge and Baker, 1990: 5, 6). See comments under footnote "j".

[i] Documented by Zanchin, under the name *O. capito*, in a Master's Thesis sponsored by the Universidade Federal do Rio Grande do Sul, Porto Alegre, 1988, which we have not seen. Zanchin's results are reported by Svartman and Almeida (1992).

[j] Based on eight specimens that show "nine centric fusion polymorphisms" (Kerridge and Baker, 1990: 5). G-banded karyotypes of three of those animals are illustrated by Koop et al. (1983). Chromosomal characteristics of these eight specimens, plus the two examples of *O. megacephalus* mentioned in footnote "f" above, were originally described as being "from a single population which contains at least nine different centric fusion/fission polymorphisms. Variation is so extensive that no two individuals had the same karyotype" (Koop et al., 1983: 131). "The exact species identification," noted Koop et al., "of this population is still under study; it is a member of the *macconnelli–capito* complex but may represent an undescribed taxon." The report is a good example of published information based upon uncritical sorting and identification of voucher specimens; careful sorting and identification are primary responsibilities of a systematic mammalogist and a requisite first step in any study designed to document analyses of data derived from the voucher material. Shortly after Koop et al. was published, Gardner examined the series and sorted them into two species. Subsequently, Musser was at Carnegie Museum, studied the same series, and made the same determinations as Gardner. The identifications were independent because Musser did not look at labels bearing Gardner's notations until after he had made his determinations. Out of the 10 specimens, both of them identified the same two as *O. "capito"* and the remaining eight as *O. yunganus*, the same combination that was eventually recognized by Kerridge and Baker (1990) in their report of allozymic variation within what they acknowledged as two species. The specimens could have been sorted before Koop et al. (1983) was published simply by using the distinguishing traits described by Gardner and Patton (1976).

[k] Reported under the name *O. bombycinus*.

[l] From their chromosomal preparations, Gardner and Patton (1976:9) could not determine "the unequivocal identification of the morphologies of all the chromosomes" obtained from the single specimen of *O. macconnelli* they reported.

[m] Results reported as *O. nitidus* by Silva (1994:9), who also summarized conclusions in Zanchin's unpublished thesis where karyotypes of $2n = 80$ and $2n = 80/81$ (FN = 86) were reportedly derived from samples identified as *O. nitidus* obtained in the Brazilian states of Bahia, Espírito Santo, and Rio Grande do Sul. In Silva's karyotype ideograph there is another biarmed pair that could be interpreted as a submetacentric or subtelocentric, which would change the FN to 88.

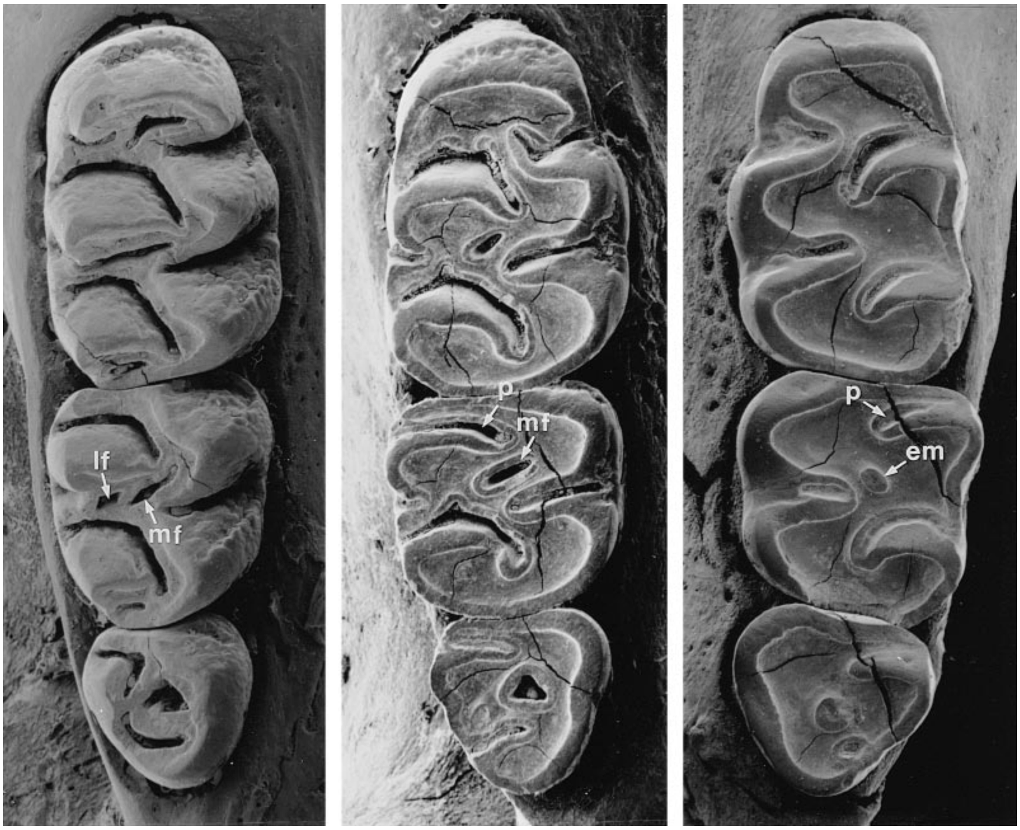

Fig. 33. Occlusal views of upper molars of *Oryzomys yunganus* depicting changes in occlusal patterns associated with age. **Left,** Young adult, Ecuador (AMNH 68118); **middle,** adult, Perú (AMNH 73182); **right,** old adult, Ecuador (AMNH 66796). Note changes in the second molar. Medial (**mf**) and labial (**lf**) fossettes are clear in the young adult. At a later age, wear has obliterated the labial fossette, leaving a short paraflexus (**p**) and elongate medial fossette. Occlusal surfaces are nearly basins in old adults and the medial fossette has been transformed into a low but conspicuous enamel mound (**em**).

of each species were collected in the same trapline in French Guiana (R. S. Voss, personal commun.), at Balta in eastern Perú (Gardner and Patton, 1976), and at sites in undisturbed terra firme and várzea forests as well as second growth along the Rio Juruá in western Brazil (J. L. Patton, personal commun.; letter in AMNH Mammalogy Archives).

Geographic ranges of *Oryzomys yunganus* and *O. macconnelli* may also be congruent. Samples of the two species have been collected from localities in the western portion of its range (in Perú, Ecuador, Colombia, and western Brazil), Venezuela, and in the eastern part (in Pará and Amapá, Brazil). Furthermore, the distribution of *O. macconnelli,* like *O. yunganus,* covers the Amazon Basin and Guiana Region (see map in fig. 78). Sympatric samples of *O. nitidus* and *O. yunganus* are too few to substantiate the same generalization, and the former is unknown from north of the Amazon River (see map in fig. 79). However, the distribution of collection localities where both species have been taken (western Perú, Bolivia, the states of Acre and Mato Grosso in Brazil) suggests that the geographic ranges of *O. nitidus* and *O. yunganus* may also overlap more extensively than is indicated by available specimens.

Oryzomys yunganus may co-occur with *O.*

TABLE 14

Descriptive Statistics for Measurements (mm) of *Oryzomys macconnelli*, *Oryzomys nitidus*, *Oryzomys yunganus*, and *Oryzomys megacephalus* from Balta, Perú (locality 49 in gazetteer for *O. yunganus*)

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. Three samples range in age from young to old adults. Specimens measured are identified in the footnotes. Statistics for lengths of head and body, tail, and hind foot are based on reliable measurement values obtained by A. L. Gardner and J. L. Patton from freshly caught animals.)

	O. macconnelli[a]	*O. nitidus*[b]	*O. yunganus*[c]	*O. megacephalus*[d]
LHB	136	136.8 ± 7.27 (121–148) 18	117.0 ± 6.83 (110–126) 4	129.7 ± 10.80 (112–148) 21
LT	134	126.8 ± 10.03 (108–147) 17	117.5 ± 9.40 (108–127) 4	114.0 ± 7.08 (102–129) 17
LHF	32	32.6 ± 1.38 (31–36) 18	30.3 ± 1.89 (29–33) 4	30.8 ± 1.50 (29–35) 22
ONL	33.1	33.6 ± 1.25 (31.3–35.6) 18	31.5 ± 2.49 (28.8–34.8) 4	32.9 ± 1.78 (29.9–36.3) 22
ZB	16.8	17.0 ± 0.67 (15.8–18.1) 18	16.4 ± 0.99 (15.4–17.7) 4	16.6 ± 0.86 (15.2–18.2) 22
IB	5.0	5.1 ± 0.20 (4.7–5.4) 19	5.2 ± 0.17 (5.0–5.4) 4	5.1 ± 0.26 (4.4–5.8) 22
LR	11.1	11.2 ± 0.59 (10.3–12.2) 19	10.3 ± 0.90 (9.3–11.1) 4	10.4 ± 0.83 (9.2–11.9) 22
BR	6.4	6.3 ± 0.49 (5.5–7.0) 19	6.2 ± 0.37 (5.7–6.6) 4	6.3 ± 0.44 (5.6–6.9) 22
LB	12.8	12.5 ± 0.42 (11.9–13.2) 19	12.3 ± 0.40 (11.9–12.9) 4	12.1 ± 0.55 (11.3–13.1) 22
HBC	9.3	9.0 ± 0.29 (8.6–9.5) 18	8.7 ± 0.29 (8.4–9.1) 4	8.9 ± 0.41 (8.3–9.9) 22
BZP	3.5	4.0 ± 0.33 (3.4–4.4) 19	3.7 ± 0.50 (3.0–4.2) 4)	3.6 ± 0.44 (2.8–4.4) 22
LD	8.8	8.5 ± 0.42 (7.7–9.1) 19	7.7 ± 0.76 (6.9–8.7) 4	8.4 ± 0.59 (7.4–9.6) 22
LBP	7.7	6.7 0.34 (6.2–7.3) 19	6.6 ± 0.75 (5.6–7.3) 4	7.4 ± 0.43 (6.5–8.1) 22
PPL	10.9	11.4 ± 0.54 (10.5–12.2) 18	10.5 ± 0.91 (9.5–11.4) 4	10.9 ± 0.70 (9.8–12.6) 22
LIF	5.1	5.7 ± 0.25 (5.3–6.2) 19	5.0 ± 0.24 (4.7–5.5) 4	4.5 ± 0.31 (4.0–5.2) 22
BIF	2.7	2.2 ± 0.13 (1.9–2.4) 19	2.1 ± 0.13 (1.9–2.2) 4	2.4 ± 0.14 (2.2–2.7) 22
CLM1-3	5.2	4.9 ± 0.12 (4.8–5.2) 19	5.0 ± 0.14 (4.9–5.2) 4	5.0 ± 0.13 (4.8–5.3) 21
BM1	1.5	1.4 ± 0.07 (1.3–1.6) 19	1.4 ± 0.05 (1.4–1.5) 4	1.4 ± 0.05 (1.4–1.5) 21

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[a] LSUMZ 14355 (adult).

[b] LSUMZ 12333, 12335–12343, 14356, 14357, 14365, 16690; MVZ 136573, 136574, 136576, 136578, 136588.

[c] LSUMZ 16685, 16687, 16689; MVZ 136585.

[d] LSUMZ 12348–12352, 12356, 12358, 14359, 16680, 16682–16684, 16692; MVZ 136575, 136577, 136579, 136580, 136582–136584, 136586, 123589.

talamancae[3] in western Venezuela in the forested strip extending between the Cordillera de Mérida and the Llanos of the Orinoco, an area that has not received much survey attention for small mammals. We have not seen any specimens of *O. talamancae* from there, but Ochoa et al. (1988b) recorded it from that region at the Reserva Forestal de Ticoporo between 250 and 260 m in Estado de Barinas. We also have documented specimens from eastern foothills of the Cordillera Oriental in Departamento de Boyacá, northern Colombia (localities 68 and 69 in gazetteer for *O. talamancae*; see map in fig. 66). *Oryzomys yunganus* has been taken at Guaicaramo (locality 18) in Departamento de Cundinamarca, Colombia, which is about 500 km southwest of the Reserva Forestal de Ticoporo. The two localities are, or at least were, connected by tropical and subtropical forest habitats (see the maps in Haffer, 1967; Hueck and Seibert, 1981; Voss, 1991: 86).

GEOGRAPHIC VARIATION WITHIN THE *ORYZOMYS YUNGANUS* GROUP

We present two sets of results here. The first examines morphological variation among samples from throughout the range of *O. yunganus*; included is the Palmera Sample, which we did not discuss in the preceding sections. The second set examines the effect, if any, of the Rio Juruá in western Brazil on geographic variation as indicated by the pattern of cranial and dental variation among samples from the same sides of that river as well as from the opposite banks.

GEOGRAPHIC VARIATION WITHIN AMAZONIA

As we separated specimens of *O. yunganus* from other species of *Oryzomys* in collections of museums, we were impressed with the appreciable variation in body size that seemed to be related to geography: large animals were from western portions of the Amazon Basin, smaller rats came from the Guiana Region and central and eastern segments of the Basin in Brazil. At first we thought the samples from the Guiana Region might represent a different species. Our view was reinforced by variation in frequency of hypothenar pads and in chromosomal traits. Most specimens from the western rim of the Amazon Basin have six plantar pads, but the hypothenar is absent in about half of the sample from French Guiana (table 7). Known variation in diploid number is slight in western samples ($2n = 58$ or 60) but great in samples from the Guiana Region ($2n = 52$–59; table 13).

We came to realize that these data were not useful for assessing significance of the geographic variation we noticed. Variation in chromosome number and morphology in *O. yunganus* has been documented by only four samples (table 13): one from Balta, Perú (locality 49), a second from San José, Perú (locality 51), another from the Tafelberg region in Surinam (locality 10), and a fourth from the Rio Juruá in western Brazil. These areas constitute a very small part of the geographic range. Frequency of occurrence of the hypothenar pad in samples is uninformative because our survey revealed that only the sample from French Guiana was unique in the high number of individuals without a hypothenar pad (table 7). We also surveyed qualitative traits associated with the skin, skull, and dentition for all samples but could not detect significant geographic variation among most of them. Basically, specimens of *O. yunganus* are alike in color and texture of the pelage as well as shape of skull and molars regardless of where collected. The Palmera Sample from central Ecuador (Mirador, Palmera, and Mera; localities 25–27 in gazetteer) is an exception. The dark pelage of these specimens and their robust molars along with qualitative cranial characteristics set the sample apart.

We turned to metric data from the samples

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[3] We do not contrast the morphological traits of *O. yunganus* and *O. talamancae* because no examples of the two have ever been collected at the same location, and their geographic ranges do not seem to overlap. Except that occlusal surface patterns of second upper and lower molars are similar to those in *O. megacephalus*, *O. talamancae* otherwise resembles *O. nitidus* in pelage coloration, conformation of cranium and mandibles, and carotid circulatory pattern, and differs from *O. yunganus* in much the same way as does *O. nitidus*. The combination of somber pelage, lack of sphenofrontal foramen and squamosoalisphenoid groove, presence of medial fossette in the second upper molar, and short hypoflexid in the second lower molar distinguishes *O. yunganus* from *O. talamancae* (see fig. 151 where variation in carotid circulatory pattern and molar occlusal pattern among species is illustrated).

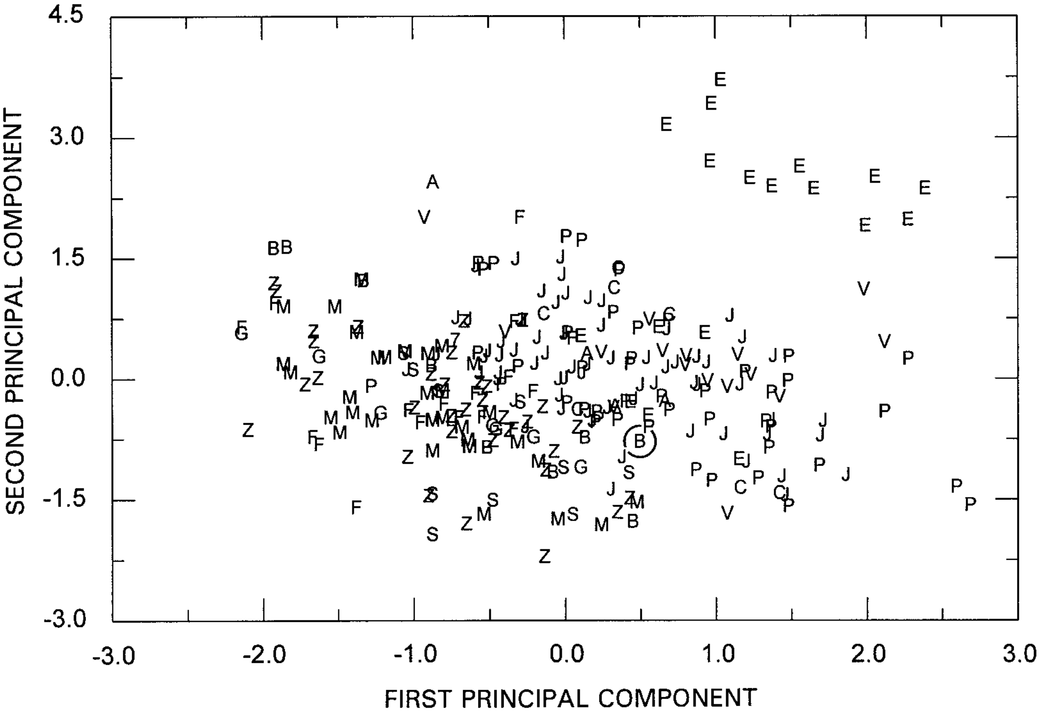

Fig. 34. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 15) and projected onto the first and second principal components extracted from analysis of old to young adult *Oryzomys yunganus* (*N* = 268). Letters represent specimens from French Guiana (F); Surinam (S); Guyana (G); Venezuela (V); Colombia (C); Ecuador (E); Perú (P); Bolivia (B); Brazil, Acre (A); Brazil, Rio Juruá (J); Brazil, Mato Grosso (M); and Brazil, Pará and Amapá (Z). Cluster of 12 Es in upper righthand area of graph indicates specimens from Palmera, Mera, and Mirador in central Ecuador. Circle identifies score representing holotype of *O. yunganus*. Results are discussed in text.

and subjected them to multivariate analyses to explore geographic patterns in variation of cranial and dental dimensions. We examined results from three analytical perspectives: (1) principal components analysis of all specimens measured of *O. yunganus* and those in the Palmera Sample, (2) discriminant function and cluster analyses of 20 population samples (identified in table 16), and (3) principal components analyses of exemplar samples of *O. yunganus* that highlight variation along two geographical transects.

In principal components analysis of 268 adults (fig. 34), the spread of specimen scores along the first component is influenced by variation in nearly all cranial and dental measurements, especially by variation in breadth of the zygomatic plate (table 15). Dispersion along the second principal component is primarily affected by variation in length and breadth of incisive foramina, length of molar row, and breadth of first upper molar; variation in breadth of rostrum and length of diastema also affects the distribution of scores, but not as strongly. The 12 specimens in the Palmera Sample (examples from Mirador, Palmera, and Mera in Ecuador; localities 25–27, respectively) form a cluster that is set apart. Their isolation reflects their large skulls, long toothrows and wide molars (means of toothrow length and molar breadth for the Palmera Sample are greater than those for any other sample analyzed—see appendix C), and short and narrow incisive foramina relative to size of cranium. The toothrow is not only long in absolute measurements but also long relative to occipitonasal length. The molars (indexed by

TABLE 15
Results of Principal Components Analysis of Adult *Oryzomys yunganus*
(Component loadings most strongly influencing dispersion of scores are in boldface. Specimens, including the holotype, are from French Guiana, Surinam, Guyana, Venezuela, Colombia, Ecuador, Perú, Bolivia, and Brazil. See fig. 34.)

	Principal components	
Variable	First	Second
ONL	**0.044**	−0.003
ZB	**0.051**	0.003
IB	0.023	0.007
LR	**0.048**	−0.005
BR	**0.051**	**−0.022**
LB	0.035	0.001
HBC	0.024	0.005
BZP	**0.066**	0.019
LD	**0.045**	**−0.025**
LBP	**0.046**	0.015
PPL	**0.053**	−0.009
LIF	**0.041**	**−0.037**
BIF	**0.044**	**−0.031**
CLM1–3	**0.049**	**0.035**
BM1	**0.041**	**0.046**
Eigenvalue	0.031	0.008
% Variance	49.4	12.2

breadth of the first upper molar) also appear more massive relative to length of molar row as compared with specimens in other samples.

Within the large primary cluster (fig. 34), scores from specimens collected in the Guiana Region (Guyana, Surinam, French Guiana, and Estado do Amapá in Brazil), eastern portions of the Amazon Basin in Brazil, and east-central Bolivia (Santa Cruz) are concentrated in the lower left quadrant of the graph. All others—representing specimens from tepuis and western margin of the Amazon Basin (southern Venezuela south through Colombia, Ecuador, Perú, and parts of Bolivia)—nestle in the upper right quadrant. Most specimens from the Guiana Region and eastern portion of the Amazon Basin have smaller crania and molars, and those from the tepuis and western Amazonia tend to be larger. However, there is substantial intermixing without clear subdivisions.

These contrasts in cranial and dental features revealed by principal components results mirror our first impression of the variation among samples as we sorted and measured specimens. Examples of the magnitude of that cranial and dental variation are illustrated in figure 35 by a cranium from the Palmera Sample as compared to one from western Amazonia and another typifying the small-bodied populations in eastern Amazonia.

Plotted results of discriminant function analysis (fig. 36) provide succinct outlines of the intersample variation indicated by qualitative inspection of crania and principal components performance. This analysis is based on the 20 composite population samples described in table 16 (descriptive statistics for each sample are listed in appendix C and specimens measured are identified in appendix D). Nearly all cranial and dental variables, particularly in length of molar row and breadth of first upper molar, influenced the distribution of the 264 specimen scores (fig. 36) and their group centroids (fig. 37) projected onto the first canonical variate extracted from the discriminant function analysis; breadth of rostrum, length of diastema, and shape of incisive foramina supply less discrimination along this axis (see insert, fig. 37, and table 17). Dispersion along the second canonical variate largely reflects variation in breadths of interorbit and zygomatic plate, lengths of diastema and bony palate, and shape of incisive foramina; variation in length of molar row and breadth of first molar is less influential. The combination of large cranial size, long toothrows and wide molars, relatively shorter and narrower incisive foramina, and a correspondingly longer bony palate isolates specimens in the Palmera Sample as a discrete constellation (fig. 36). The distance between Palmera's centroid and any other group's centroid exceeds that derived for all other intersample comparisons of morphometric divergence (fig. 37).

The primary cluster of individual specimen scores is weakly subdivided into two geographic aggregations. One represents examples from the Guiana Region and eastern portion of the Amazon Basin in Brazil; the other indicates specimens from Western Amazonia and the tepuis of eastern Venezuela. Overlap between the two groups is apparent but not pronounced. The score of the

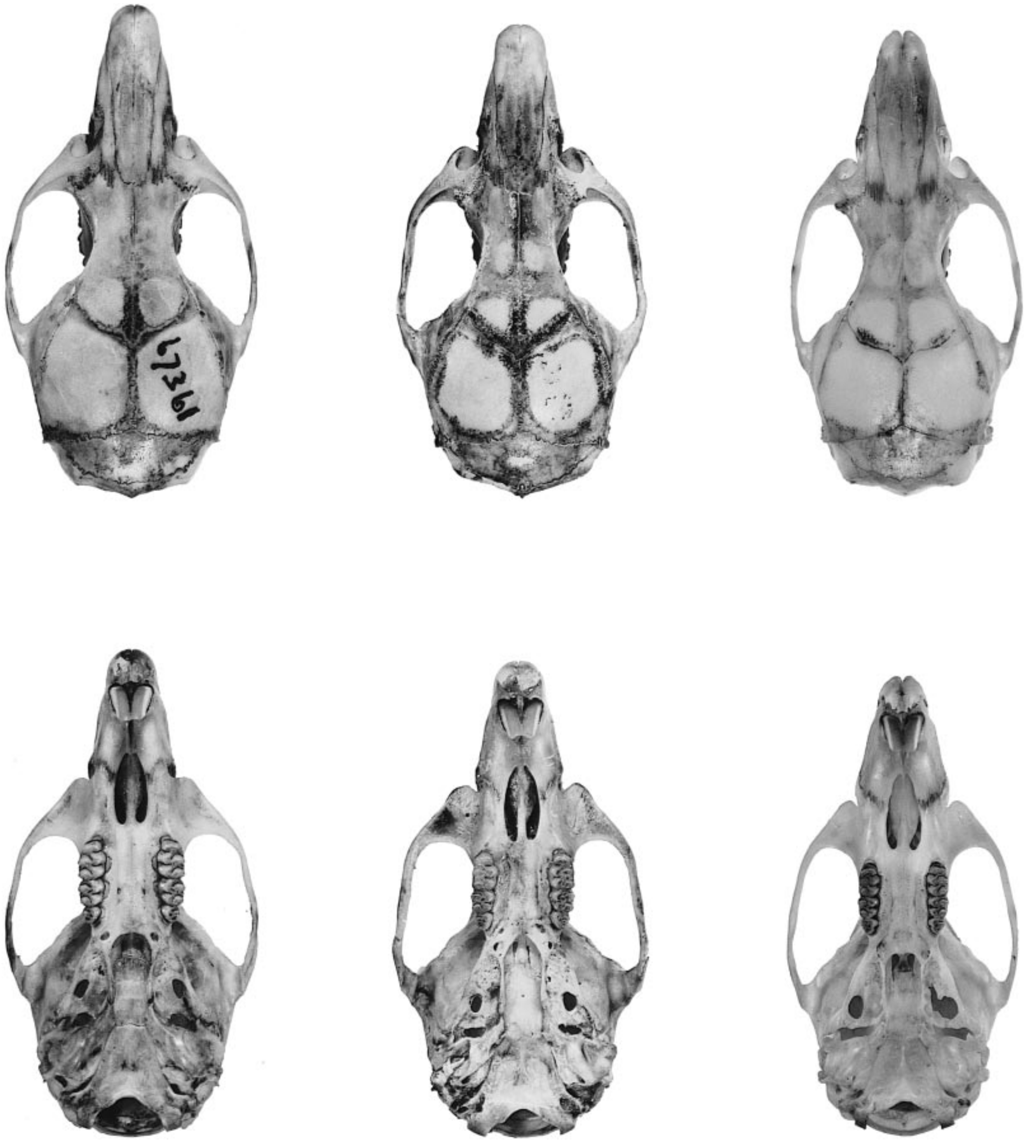

Fig. 35. Dorsal (top row) and ventral (bottom) views of adult crania illustrating representatives of the *Oryzomys yunganus* group from the Palmera Sample (**left**), tepuis and western Amazonia (**middle**), and the Guiana region and eastern Amazonia (**right)**. From right to left: AMNH 67361 from Palmera, Ecuador (locality 26 in gazetteer); AMNH 68106 from San José Abajo, Ecuador (locality 23); and USNM 521521 from west of Altamira, Brazil (locality 80). ×2.

holotype of *O. yunganus,* derived from posterior probabilities of group membership, associates it with the tepui and western Amazonian specimens, but not with those at the heart of that aggregation.

The distribution of group centroids (fig. 37) illustrates two other aspects of cranial and dental variation that we noticed while sorting and measuring specimens. First, specimens from French Guiana (sample 1) are not only small in cranial and dental size, but they also have relatively shorter and narrower incisive foramina than do most other samples; the Palmera Sample, although opposite in

TABLE 16

Population Samples of the *Oryzomys yunganus* Group Used in the Multivariate Analyses

(Each sample ranges in age from young to old adults. Descriptive statistics for each sample are listed in appendix C; specimens measured are identified in appendix D. Total N = 264.)

	Sample	N	Locality (number and name key to localities in gazetteer for *O. yunganus*)
1.	FRENCH GUIANA	18	1. Arataye
			3. Île de Cayenne
			5. Paracou
2.	SURINAM	11	10. Tafelberg
			11. Kaiser Gebergte Airstrip
3.	GUYANA	7	12. Kwabanna
			13. Santa Cruz
4.	VENEZUELA: Bolívar	14	14. Auyán Tepuy
			15. Arabopó
5.	COLOMBIA: Central	6	18. Guaicaramo
			18a. Villavicencio
			18b. Serranía de La Macarena
6.	ECUADOR: Napo + E Pastaza	7	22. Llunchi
			23. San José Abajo
			30. Río Tigre
7.	ECUADOR: Tungurahua + W Pastaza	12	25. Mirador
			26. Palmera
			27. Mera
8.	PERÚ: Northern	16	33. Huachi
			35. Yambrasbamba
			36. Yambra
			38. Puca Tambo
			40. Moyobamba
9.	PERÚ: Central	9	43. Río Chinchao
			44. Chinchao
			47. Eneñas
10.	PERÚ: Southern	13	50. Reserva Cuzco Amazónico
			53. Quincemil
			54. Cadena
11.	BOLIVIA: Pando + Beni	5	56. Las Piedras
			57. Boca del Río Biata
12.	BOLIVIA: Santa Cruz	3	60. Cerro Amboró
13.	PERÚ + BRAZIL	8	49. Balta
			61. Sena Madureira
14.	BRAZIL: Acre (left and right banks Rio Juruá)	11	62. Opposite Igarapé Porongaba
			63. Porongaba
			64. Ocidente
			65. Sobral
			66. Nova Vida
15.	BRAZIL: Amazonas-1 (left bank Rio Juruá)	15	67. Seringal Condor
			69. Igarapé Nova Empresa
16.	BRAZIL: Amazonas-2 (right bank Rio Juruá)	38	68. Penedo
			71. Altamira
			73. Jainú
17.	BRAZIL: Amazonas-3 (right bank Rio Juruá)	4	74. Colocação Vira Volta
18.	BRAZIL: Mato Grosso	33	78. Serra do Roncador
19.	BRAZIL: Pará	5	79. 150 km W Altamira
			80. 19 km W Altamira
20.	BRAZIL: Amapá	29	82. Serra do Navio

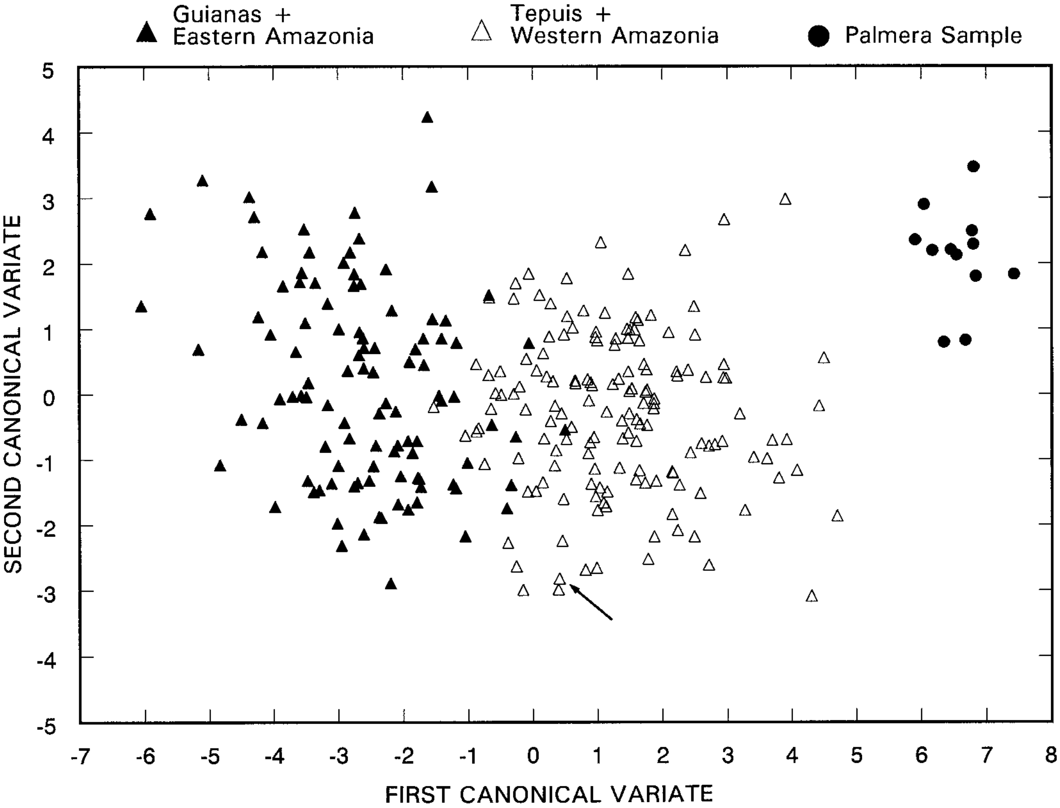

Fig. 36. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 17) and projected onto the first and second canonical variates derived from discriminant function analysis of 20 population samples representing *Oryzomys yunganus* (samples 1–6, 8–20; *N* = 252) and the Ecuadoran specimens from Mirador, Palmera, and Mera (sample 7; *N* = 12). The population samples contain 264 of the 268 specimens measured (the number used in the principal components analysis; fig. 35). The remaining five are from localities 16, 17, 20, 31, and 59 (holotype of *O. yunganus*, whose score is indicated by an arrow) in western Amazonia and were entered as unknowns to the discriminant function analysis and classified a posteriori; they are included in this scatterplot and fall within the western Amazonian cluster. See also figure 37.

size of crania and molars, exhibits similar proportions of incisive foramina (appendix C).

Second, the Bolivian samples are problematically distributed and their affinities are unclear. The centroid for the five specimens from the departments of Pando and Beni in northern Bolivia (sample 11) forms part of the western Amazonia cluster, but its marginal placement may reflect biased age composition of the sample—four out of the five individuals are young adults. The centroid for three specimens from Santa Cruz in east-central Bolivia (sample 12), as well as the score for the holotype, are not only at the left margin of the western Amazonia centroid cluster but are somewhat isolated from it along the second canonical variate. Sample 12 contains an old adult, an adult, and a young adult; the holotype is an old adult. Morphometric separation of samples 11 and 12 may only reflect their contrasting age compositions or might be an artifact of sampling. New and larger Bolivian samples are clearly desirable and may prove significant to understanding the genetic relationships between western and eastern entities of *O. yunganus* (excluding the Palmera Sample).

Position of the Bolivian samples varies relative to the others in clustering patterns

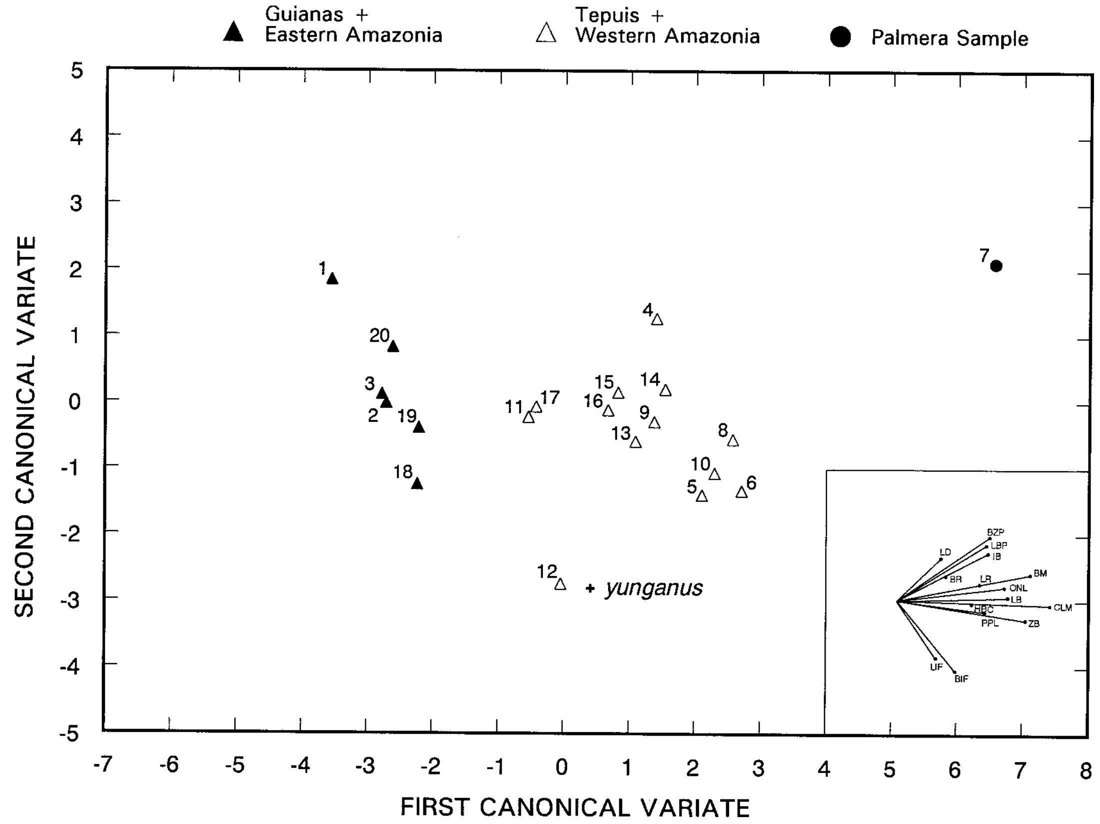

Fig. 37. Plot of group centroids on first two canonical variates derived from discriminant function analysis of 20 population samples representing *Oryzomys yunganus* (samples 1–6, 8–20) and the Ecuadoran specimens from Mirador, Palmera, and Mera (sample 7). See also figure 36. Score of holotype of *O. yunganus* derived from posterior probabilities of group membership is also shown. **Inset:** Vectors of 13 cranial and 2 dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (see table 17). Sample sizes and the localities that constitute each are listed in table 16.

based on Mahalanobis' (the generalized distance between centroids over all canonical variates derived, thus providing more information than can be seen in score scatter on the first two canonical variates) and Euclidean distances (using log-transformed sample means of 13 cranial and 2 dental variables) (figs. 38, 39). In both diagrams, the distinctiveness of the Palmera Sample is striking. Samples from the Guiana Region and eastern margin of the Amazon Basin form a tight aggregation in the Mahalanobis' configuration that is clearly separate from the cluster consisting of samples from tepuis and western Amazonia. Pair-group associations within the latter cluster reflect expected relationships based on geographic proximity. Series from along the Rio Juruá (samples 14–17), for example, cluster closer to one another than to other samples. Furthermore, the two Bolivian samples (11 and 12) form a discrete association, but one that is still part of the larger western Amazonian group.

The phenetic association of population samples from the Guiana Region and eastern Amazon Basin apart from those in western Amazonia is also expressed in the Euclidean pattern. Membership of subunits within each primary aggregation differs, particularly the placement of the Bolivian samples. Examples from Pando and Beni in northern Bolivia (sample 11) associate with those from the

TABLE 17
Results of Discriminant Function Analysis of 20 Population Samples of *Oryzomys yunganus* (Samples 1–6, 8–20) and the Sample from Palmera, Mirador, and Mera (Sample 7)
(Localities constituting each sample, and sample size, are listed in table 16; mean values for measurements of variables in each sample are listed in appendix C; and specimens measured are identified in appendix D. See figs. 36 and 37.)

Variable	Canonical variates First	Canonical variates Second	F (Sample)[a]
ONL	0.66	0.08	120.8
ZB	0.79	–0.12	230.5
IB	0.58	**0.29**	100.7
LR	0.51	0.10	60.2
BR	0.30	0.15	40.5
LB	0.68	0.02	140.2
HBC	0.46	–0.02	50.5
BZP	0.57	**0.39**	100.1
LD	0.27	**0.26**	40.9
LBP	0.55	**0.34**	100.9
PPL	0.54	–0.07	80.4
LIF	0.24	**–0.35**	40.8
BIF	0.36	**–0.43**	60.6
CLM1–3	0.94	–0.03	540.2
BM1	0.82	0.16	240.2
Canonical correlation	0.93	0.73	
Eigenvalue	6.67	1.16	
% Variance	61.4	10.7	

[a] All F values are significant at $P < 0.001$.

Guianas and eastern Amazonia, but the series from farther south in Santa Cruz forms an outlier of the western Amazonia group.

Excluding the Palmera series, the other samples of *O. yunganus* fall into two geographic groups, defined primarily by size of certain cranial and dental dimensions and proportions. Morphological variation among these clusters, as judged by available specimens, does not overlap in northern Amazonia (perhaps reflecting two distinct biological entities) but suggests intergradation in the Amazon Basin. We illustrate this pattern by principal components analyses of two sets of samples. The first contrasts specimens characterized by large crania and molars from a tepui in eastern Venezuela with smaller specimens collected in Guyana and Surinam (fig. 40; table 18). Specimen scores along the first principal component segregate into two nearly exclusive clusters influenced by variation in nearly all cranial and dental measurements but especially by breadths of rostrum, zygomatic plate, and incisive foramina followed by lengths of bony palate, postpalatal region, and molar row. This configuration of scores, obscured in the principal components analysis of all 268 specimens (fig. 34), reflects the striking differences in size between crania and toothrows of the tepui samples in eastern Venezuela and those from the Guiana Region (see descriptive statistics in appendix C). By using overall cranial and molar size as a distinguishing feature, the two sets of specimens in northern Amazonia have the aspect of different species. However, no samples are available from the region between the eastern tepuis of Venezuela and the lowlands of northern Guyana and Surinam, so we are ignorant about the nature of variation over this gap. To determine the biological significance of the morphological differences in this region, future surveys should focus along transects extending from the tepuis in eastern Venezuela northward through Guyana to the coast or eastward through Guyana to Surinam. These surveys would determine if the larger bodied western Amazonian segment is restricted to tropical evergreen rain forest on the tepuis and the smaller bodied Guianan populations are confined to lowland forest (with each maintaining their genetic and morphological distinction) or if the two apparent size classes actually intergrade somewhere in eastern Venezuela and Guyana.

Our second principal components analysis compares variation between a sample from western Brazil along the Rio Juruá and the sample from Serra do Roncador in southeastern Amazonia. The dispersion of specimen scores along the first principal component is affected by variation in all variables, with eight having more influence than the others (fig. 40; table 18); however, the spread, both along this axis and the second principal component, forms two overlapping clusters. The pattern mimics that resulting from principal components analysis of all 268 specimens (fig. 34): the smaller crania (most from Serra do Roncador in eastern Amazonia) are represented by scores in the left part of the cluster, the larger specimens

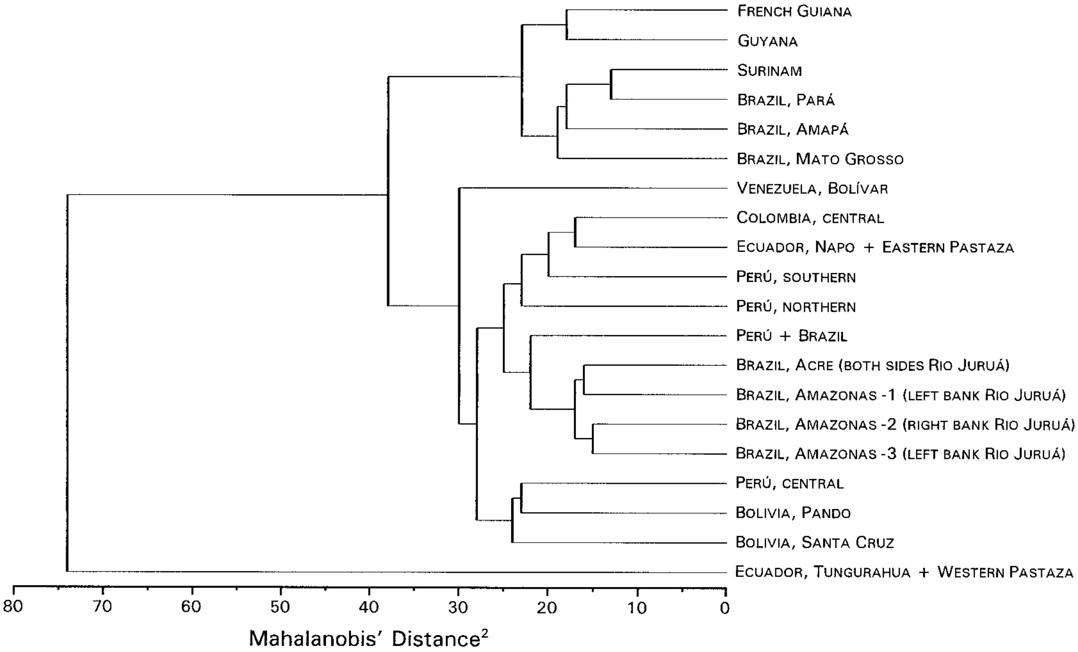

Fig. 38. UPGMA clustering of population samples of *Oryzomys yunganus* (samples 1–6, 8–20) and the Ecuadoran specimens from Mirador, Palmera, and Mera (sample 7) generated from Mahalanobis' distances (D^2) among group centroids (see fig. 37). Contrast this cluster pattern with that shown in figure 39 on opposite page. Geographic origin and size of each sample are indicated in table 16, mean values for measurements of variables are listed in appendix E, and specimens measured are identified in appendix F.

(the bulk from the Rio Juruá in western Amazonia) by scores in the right half, and there is no discrete division between them. Clearly, a line across the Amazon Basin from its western to eastern margins defines another survey transect that might illuminate the significance of the east–west morphological overlap in cranial and dental dimensions suggested by our analyses. The vast heart of the Amazon Basin is virtually unsampled for *O. yunganus* (note the large hiatus on the map in fig. 14). We have seen only two specimens from that region. They came from the southern margin of the Basin in eastern Rondônia and western Mato Grosso (localities 76 and 77 in gazetteer and in fig. 14). Unfortunately, both are old adults with fragmented crania; upper molars are missing from one and the other retains only the first two molars in each maxillary row. Sizes of some of the larger fragments (rostrum of one specimen, anterior three-fourths of the cranium in the other) resemble those of the smaller specimens in samples from eastern Amazonia. We estimate the molar rows to have been 4.6 or 4.7 mm long, based on the remnants of the one and length of the mandibular row in the other (in which the maxillary molars are missing). These values are within the range of variation, although at the higher end, of the Serra do Roncador sample (locality 78), the closest of the eastern Amazonia localities. On the other hand, the values fall in the middle or at the lower end of samples from along the Rio Juruá in western Amazonia (see descriptive statistics listed in appendix C). Whether these individuals represent the small end of size variation in the population or are indicative of the average composition of populations in south-central Amazonia can only be determined by obtaining larger samples from that region.

Approximations of molar row lengths in the two specimens are also close to values in the two Bolivian samples (see appendix C), particularly the five specimens from the de-

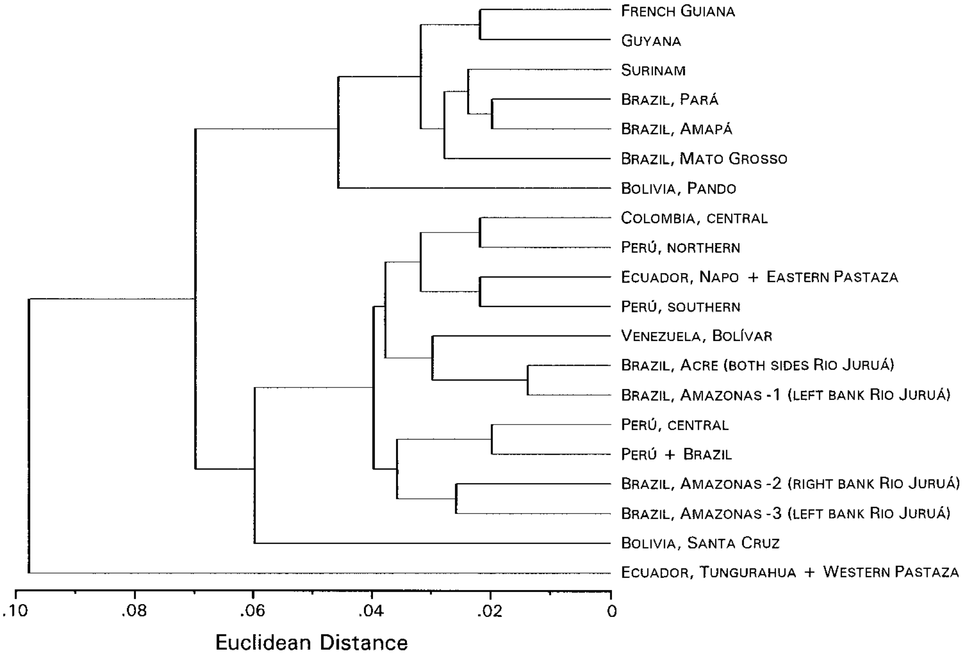

Fig. 39. UPGMA clustering of population samples of *Oryzomys yunganus* (samples 1–6, 8–20) and the Ecuadoran specimens from Mirador, Palmera, and Mera (sample 7) generated from Euclidean distances between samples based on log-transformed means of the 15 cranial and dental variables. Contrast this pattern with the cluster diagram in figure 38 on opposite page.

partments of Pando and Beni in northern Bolivia (localities 56 and 57), the western samples closest to those localities at which the two Brazilian specimens were captured. This similarity highlights the uncertain position of the Bolivian samples in our analyses. In the principal components procedure, scores for most Bolivian specimens fall in the zone between those representing specimens from eastern and western Amazonia (fig. 34). In discriminant function analysis, the Bolivian series are outliers to most western Amazonia samples, whether as seen in the canonical variate scatterplot of group centroids (fig. 37) or in the phenogram using Mahalanobis' distances (fig. 38). However, clustering of log-transformed sample means weakly associates one Bolivian sample with series from the Guianas and eastern Amazonia and the other with the western Amazonia samples (fig. 39). In this analytical context, the Bolivian samples either represent smaller individuals at the southern margin of the western Amazonia segment, larger bodied specimens in the westernmost part of the eastern Amazonia distribution, or genetic intermediates between western and eastern populations.

As a provisional hypothesis, we consider the cranial and dental variation documented among the available samples (again excepting the Palmera Sample) to reflect geographic variation within one species, *O. yunganus*. Our judgment is founded on uncertainty about the real relationships of the Bolivian samples; the apparent overlap in range of morphometric variation between samples from western and eastern margins of the Amazon Basin; and lack of specimens from critical geographic regions in northern Amazonia, the core of the Amazon drainage, and southern Amazonia in Bolivia and adjacent Brazil. More samples from Bolivia are especially important for understanding the genetic relationships between eastern and western segments.

We accept the hypothesis that specimens from Palmera, Mera, and Mirador represent a biological species distinct from *Oryzomys yunganus*. The uniqueness of the Palmera Sample is consistently underscored in prin-

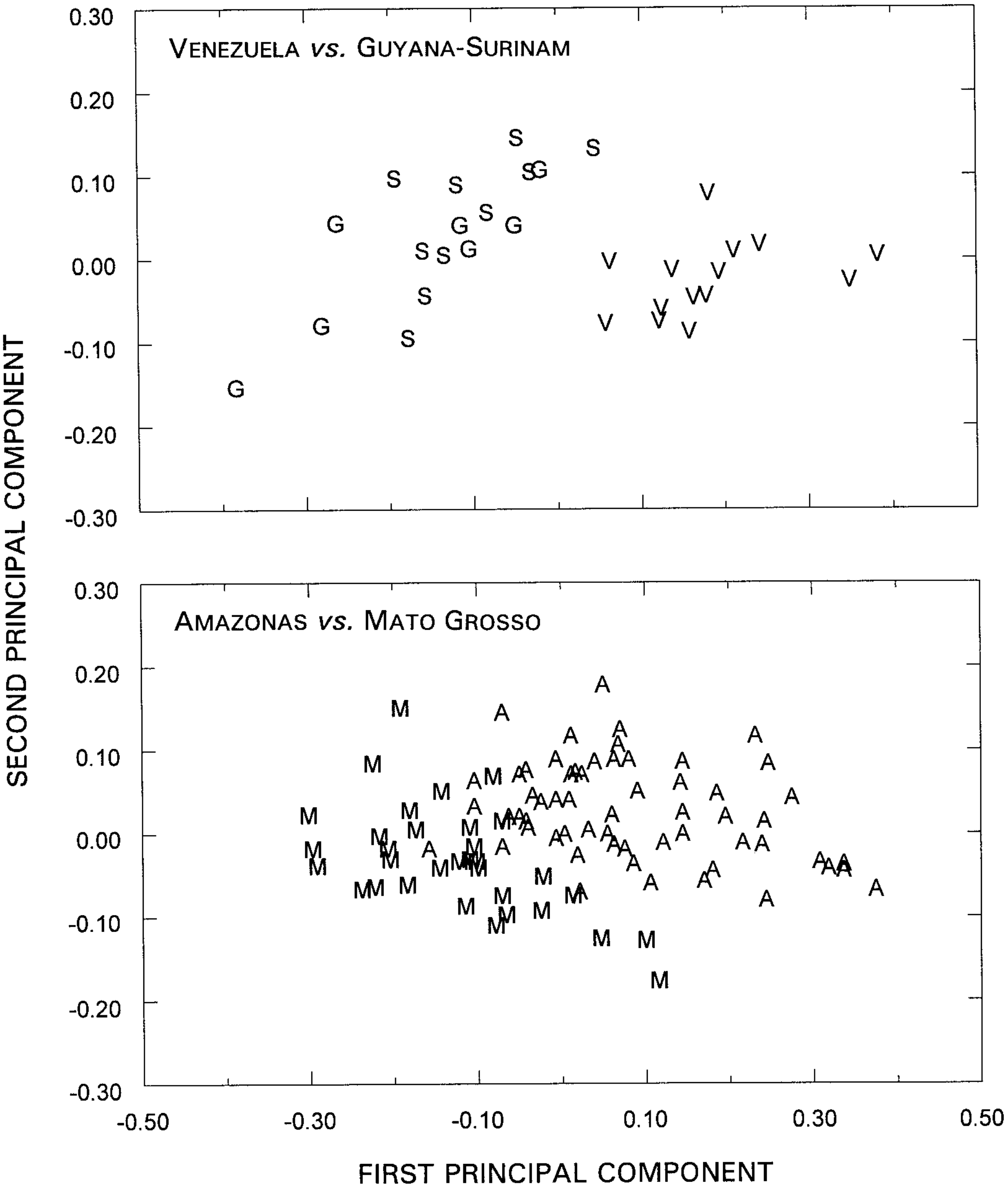

Fig. 40. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 18) and projected onto the first and second principal components extracted from analysis of young to old adult *Oryzomys yunganus*. **Top**: Samples from Venezuela (N = 14) contrasted with those from Guyana and Surinam (N = 17). **Bottom:** Samples from Amazonas, along the Rio Juruá in western Brazil (N = 59), contrasted with one from Mato Grosso at Serra do Roncador in eastern Brazil (N = 33). Significance of these distributions is discussed in text.

cipal components, discriminate function, and cluster analyses (figs. 34, 36–39). Its isolation in these multivariate patterns reflects the distinctive morphological traits common to the sample: a combination of large cranial size, relatively small incisive foramina, and robust molars. We name and characterize it as a new species following the account of *O. yunganus.*

TABLE 18
Results of Principal Components Analyses of Adult *Oryzomys yunganus* from Venezuela, Guyana, Surinam, and the Brazilian States of Amazonas and Mato Grosso
(Component loadings most strongly influencing dispersion of scores are in boldface. See fig. 40.)

	Principal components			
	Venezuela versus Guyana and Surinam[a]		Amazonas versus Mato Grosso[b]	
Variable	First	Second	First	Second
ONL	0.035	0.011	**0.042**	0.004
ZB	0.029	0.002	**0.045**	0.008
IB	0.028	0.007	0.024	0.011
LR	0.035	0.019	**0.043**	–0.006
BR	**0.051**	**0.030**	**0.058**	–0.005
LB	0.022	0.006	0.038	0.006
HBC	0.018	–0.005	0.020	0.007
BZP	**0.104**	**–0.035**	**0.055**	0.010
LD	0.028	**0.027**	**0.057**	0.001
LBP	**0.044**	0.023	**0.041**	**0.025**
PPL	**0.069**	–0.006	**0.047**	0.000
LIF	0.022	0.022	0.029	**–0.041**
BIF	**0.064**	0.013	0.035	**–0.040**
CLM1–3	**0.064**	–0.019	0.020	0.006
BM1	0.037	–0.019	0.021	0.011
Eigenvalue	0.036	0.005	0.024	0.005
% Variance	64.2	9.7	54.3	10.1

[a] Specimens from Venezuela are from Auyán Tepuy (locality 14 in gazetteer for *O. yunganus*) and Cerro Duida (locality 16). Samples from Guyana are from Kwabanna (locality 12) and Santa Cruz (locality 13). Specimens from Surinam come from Tafelberg (locality 10) and Kaiser Gebergte Airstrip (locality 11).

[b] Specimens from Amazonas were taken along right and left banks of the Rio Juruá (localities 67–71, 73, and 74). The sample from Mato Grosso comes from Serra do Roncador (locality 78).

EFFECT OF RIVERS ON GEOGRAPHIC VARIATION

"Wide river channels and their adjacent floodplains in Amazonia are effective barrier zones for the dispersal of birds and many other animals inhabiting the interior of terra firme forest" (Haffer, 1992: 218). Our final inquiry into exploring patterns of geographic variation in *O. yunganus* was to compare samples from either side of the Rio Juruá. To this analysis we also brought data from samples of *O. megacephalus* collected along banks of the same river. Recently, Patton et al. (1994) examined sequence variation in the mitochondrial cytochrome-*b* gene in the caviomorph *Mesomys hispidus* obtained from 15 locations along the Rio Juruá, which "is a broad floodplain river, coursing nearly 1000 km from the Peruvian–Brazilian border to the south bank of the Amazon upriver from Manaus" Patton et al. (1994: 1315). Testing the "Riverine Barrier Hypothesis" (see Haffer, 1992, and Patton et al., 1994, for relevant references) was the explicit intention of Patton and his colleagues. That the Rio Juruá "might be an effective barrier for Amazonian taxa is suggested by its identification as a major avian contact zone [Haffer, 1974] and as a presumptive zone of rapid environmental transition [Brown, 1982; Endler, 1982]" (Patton et al., 1994: 1315). Lower reaches of the Rio Juruá and bordering seasonally flooded forest (várzea) do form the boundary between distinctive genotypic and phenotypic populations of saddle-back tamarins, *Saguinus fuscicollis* (Peres et al., 1996).

Patton and members of his field team collected the specimens of *O. yunganus* and *O. megacephalus* that we measured from the vicinity of the Rio Juruá. Specimens came from the four areas along the river designated by Patton et al. (1994) as: "Headwaters Area," Upper Central Area," "Lower Central Area," and "Mouth Area." By using principal components analyses (fig. 41), we contrasted cranial and dental measurements from adults collected from one side of the river with those taken on the opposite bank. The spread of specimen scores along the first and second components for each species is influenced most strongly by certain cranial measurements (table 19), but they do not coalesce into clusters. In the graph for each species, the points form one large cloud and scores representing specimens from right and left banks are thoroughly intermingled. In the

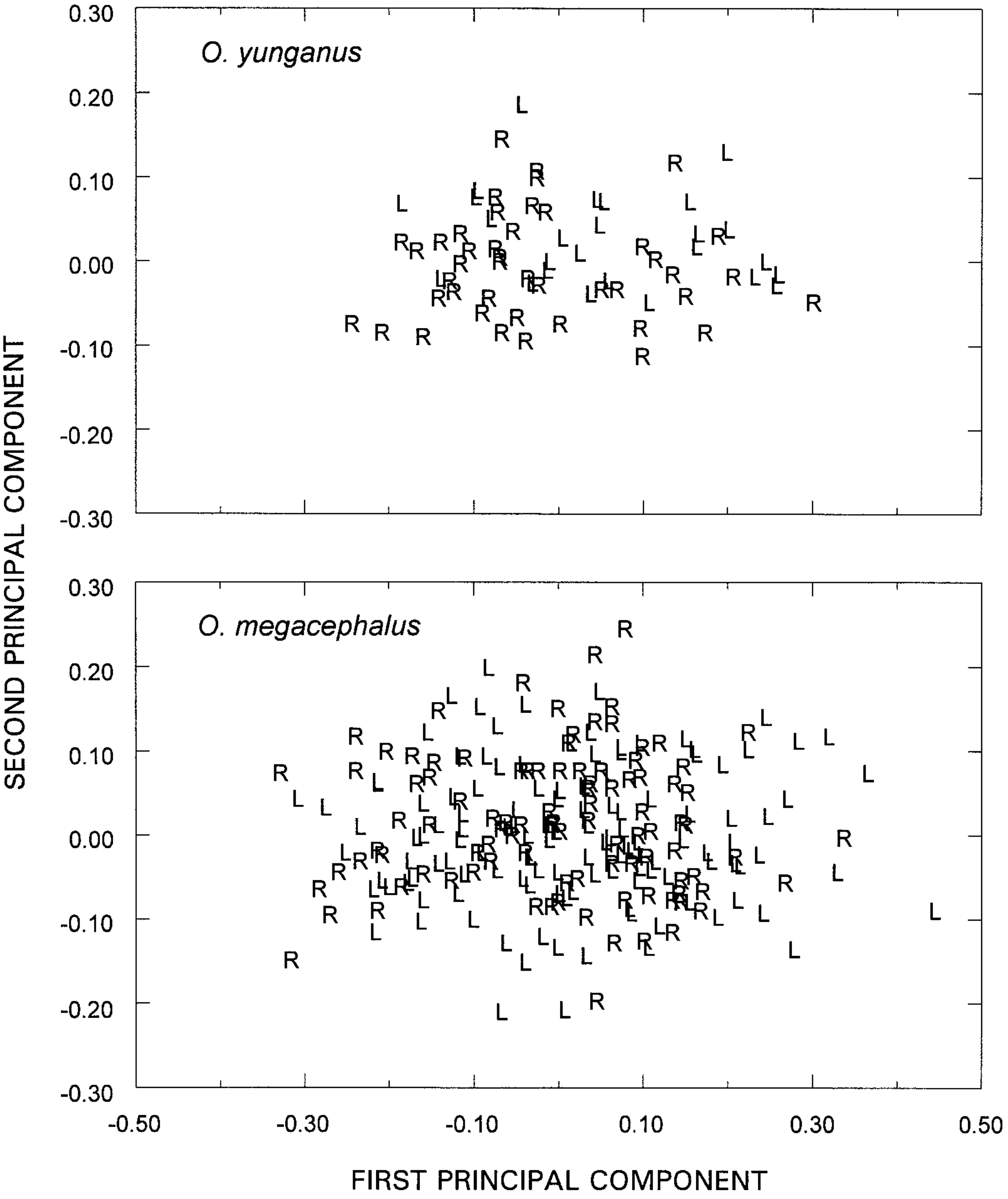

Fig. 41. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 19) and projected onto the first and second principal components extracted from analysis of young to old adult *Oryzomys yunganus* and *O. megacephalus* obtained on right (**R**) and left (**L**) banks along the Rio Juruá in Acre and Amazonas, western Brazil. **Top:** *O. yunganus*—right bank, *N* = 44; left bank, *N* = 26. **Bottom:** *O. megacephalus*—-right bank, *N* = 130); left bank, *N* = 100. Results are amplified in text.

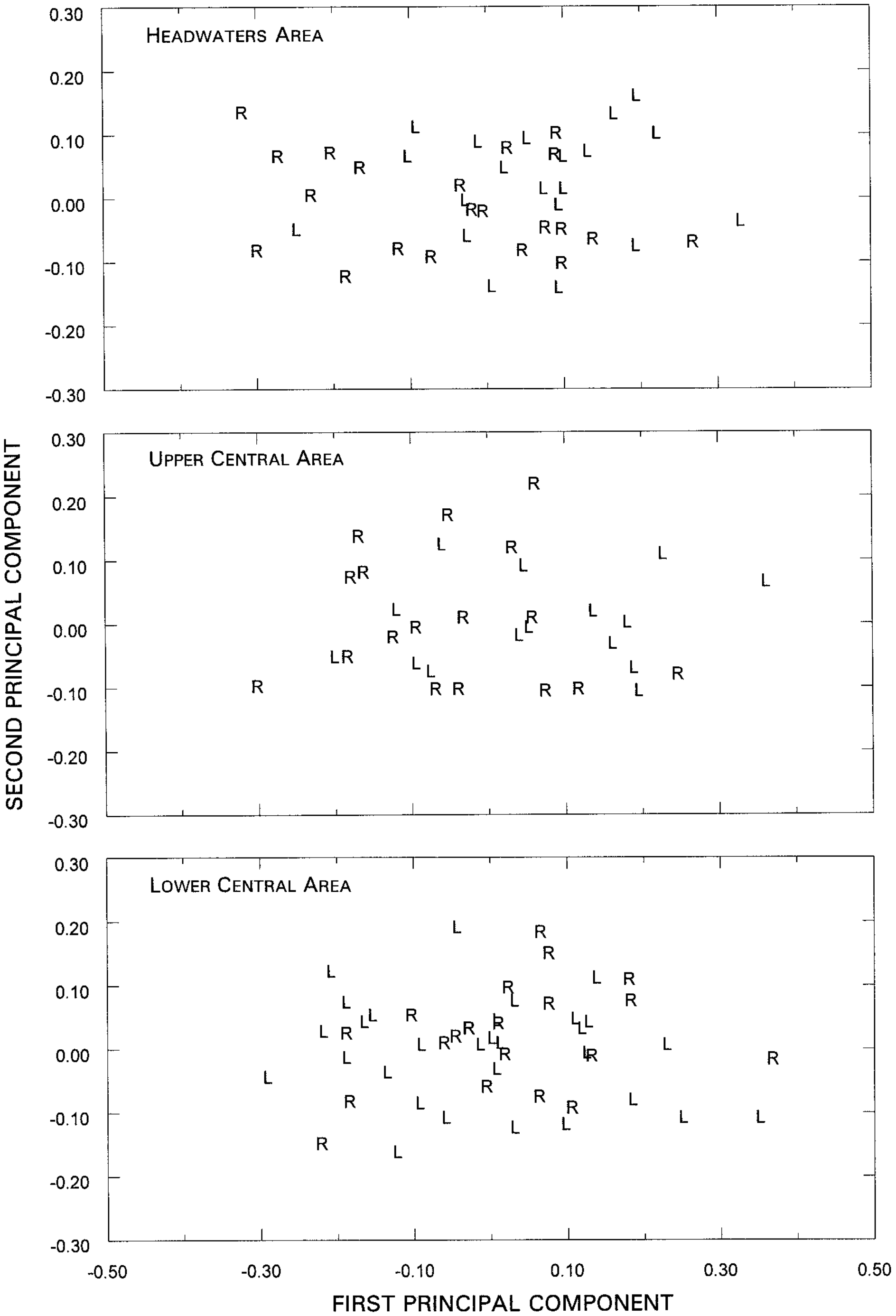

Fig. 42. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 20) and projected onto the first and second principal components extracted from analysis of young to old adult *Oryzomys megacephalus* obtained on right (**R**) and left (**L**) banks along three regions of the Rio Juruá in Acre and Amazonas, western Brazil. Headwaters Area: Porongaba on right bank (sample 23; *N* = 21), opposite Porongaba on left bank (sample 22; *N* = 20). Upper Central Area: Sacado on right bank (sample 27; *N* = 17), Condor on left bank (sample 26; *N* = 15). Lower Central Area: Altamira and Jainú on right bank (sample 31; *N* = 20), Barro Vermelho on left bank (sample 30; *N* = 30). Samples are described in table 1. See discussion in text.

TABLE 19

Results of Principal Components Analyses of Adult *Oryzomys yunganus* and *Oryzomys megacephalus* from Right and Left Banks along Rio Juruá in Acre and Amazonas, Western Brazil

(Component loadings most strongly influencing dispersion of scores are in boldface. Numbers in parentheses key to localities in gazetteer for *O. yunganus* and samples in table 1 for *O. megacephalus*. Specimens used in the analyses are listed in appendices B and D. See fig. 41.)

	Principal components			
	O. yunganus (62, 63, 65–71, 73, 74)		*O. megacephalus* (26–33)	
Variable	First	Second	First	Second
ONL	0.034	0.006	**0.037**	0.001
ZB	0.030	0.004	**0.037**	0.000
IB	0.003	–0.009	0.016	–0.011
LR	**0.043**	0.005	**0.045**	0.002
BR	**0.061**	0.011	**0.058**	0.013
LB	0.021	–0.004	0.025	0.005
HBC	0.015	0.004	0.031	0.005
BZP	**0.038**	0.009	**0.055**	0.008
LD	**0.046**	0.005	**0.052**	0.001
LBP	0.030	**0.027**	0.031	0.027
PPL	**0.038**	0.005	**0.048**	–0.001
LIF	**0.036**	**–0.044**	**0.036**	**–0.045**
BIF	**0.037**	**–0.025**	0.016	**–0.059**
CLM1–3	0.011	–0.011	0.003	0.003
BM1	0.012	–0.010	0.005	–0.001
Eigenvalue	0.017	0.004	0.021	0.007
% Variance	48.4	10.9	46.4	14.9

features related to size of cranium and molars, we detected no meaningful contrast in samples from right and left river banks in either *O. yunganus* or *O. megacephalus* when all specimens of each species are combined into two samples, one from each bank along the river from headwaters to the mouth. A similar pattern for *O. yunganus* is exhibited in the diagrams for Mahalanobis' and Euclidean distances (figs. 38, 39).

To obtain finer resolution, we compared pairs of collection localities—a site on one bank with that on the opposite bank. We used samples of *O. megacephalus* for this analysis because to sort specimens of *O. yunganus* into pairs of sites would have so reduced sample sizes that results based on them would be questionable. A large sample of adult *O. yunganus* was available only from Penedo (N = 34), one series consisted of 12 individuals, and all the other samples ranged in number of specimens from 1 to 5.

Collections of *O. megacephalus* from each locality are larger and we were able to analyze three pairs of samples: (1) Headwaters Area, Porongaba (locality 27 in table 1) and opposite Porongaba (locality 26); (2) Upper Central Area, Seringal Condor (locality 30) and Sacado (locality 31); and (3) Lower Central Area, Barro Vermelho (locality 36) and Jainú (locality 37). Samples from the Mouth Area were not included because in that region examples of *O. megacephalus* were obtained from only one side of the river. Results of principal components analyses of these three pairs of sites mirror that obtained from the analysis where all specimens were combined (fig. 42; table 20). Scores representing specimens from each pair intermingle to form a single cluster.

It is noteworthy that Patton et al. (1994: 1314) uncovered two haplotype clades from their samples of *Mesomys hispidus,* "but these correspond to headwaters versus mouth areas, not to opposite sides of the river, as would be expected by the Riverine Barrier Hypothesis. Moreover, haplotype sharing across the river was greater at its mouth than in the headwaters, a pattern opposite to that expected if the river were a substantive barrier." Our analyses also failed to demonstrate differences between samples of either *O. yunganus* or *O. megacephalus* from opposite sides of the river.

We did not have enough specimens of *O. yunganus* to investigate relationships among samples along the river from the headwaters to near its mouth. *Oryzomys megacephalus,* however, was represented by more and larger samples. Cluster analyses of sample means representing that species did not reveal a pattern suggesting samples from the headwaters to be distinct from those collected at the mouth area (fig. 43).

The absence of significant divergence between samples of *O. megacephalus* collected on opposite banks of the Rio Juruá and among samples from Headwaters Area to the Lower Central Area was also reported by Patton et al. (1996) based on their investigation of cytochrome-b sequence variation. They found that "virtually all haplotype vari-

TABLE 20

Results of Principal Components Analyses of Adult *Oryzomys megacephalus* from Right and Left Banks along Rio Juruá in the Headwaters Area, Upper Central Area, and Lower Central Area of Acre and Amazonas, Western Brazil

(Component loadings most strongly influencing dispersion of scores are in boldface. Samples are identified in table 1. Specimens measured are identified in appendix B. See fig. 42.)

	Principal components					
	HEADWATERS AREA (Samples 26 and 27)		UPPER CENTRAL AREA (Samples 30 and 31)		LOWER CENTRAL AREA (Samples 36 and 37)	
Variable	First	Second	First	Second	First	Second
ONL	0.037	0.000	0.038	0.002	0.037	0.001
ZB	0.040	0.005	0.032	−0.006	**0.045**	0.003
IB	0.022	−0.011	0.011	−0.001	0.020	−0.012
LR	0.039	0.005	**0.058**	0.011	0.038	0.000
BR	**0.064**	−0.014	**0.052**	0.004	**0.070**	−0.022
LB	0.031	−0.004	0.023	0.003	0.025	−0.006
HBC	**0.046**	0.013	0.033	0.010	0.033	−0.012
BZP	**0.066**	0.000	**0.071**	0.002	**0.056**	0.009
LD	**0.057**	0.003	**0.059**	0.002	**0.048**	−0.002
LBP	0.029	−0.023	**0.044**	0.031	0.028	−0.035
PPL	**0.056**	0.004	**0.047**	0.001	**0.054**	0.004
LIF	0.028	0.035	0.033	−0.043	0.028	**0.057**
BIF	−0.007	**0.066**	0.019	**−0.071**	0.022	0.036
CLM	0.001	−0.008	0.002	−0.005	0.005	0.002
BM	0.007	−0.005	−0.002	−0.011	0.012	0.014
Eigenvalue	0.025	0.007	0.024	0.008	0.022	0.008
% Variance	52.7	14.5	48.9	16.6	49.1	15.1

ation is contained within local populations within regions (>89%); there is little or no among-population (<6.6%) or among-region (<4.2%) contribution. . . . Virtually all (>97%) of haplotype variation is that between individuals in comparisons between Upper and Lower Central regions" (p. 234). "By any view," they wrote, "the overall pattern of haplotype diversity within *O.* [*megacephalus*] is one of little to no regional or even among-population effect" (p. 234). Patton et al. also noted that "there is no evidence of isolation by distance for this species" (p. 234).

Whether the lower courses of wide rivers such as the Amazon form significant barriers to gene flow between populations of *O. yunganus,* as well as *O. megacephalus,* is unknown. In the case of the Amazon River, we lack sufficient samples from its opposite banks to critically test the hypothesis. Although the occurrence of gene flow is indeterminate on a micrographic scale, we note that samples of both *O. yunganus* (figs. 38, 39) and *O. megacephalus* (figs. 4, 6) from north of the Amazon, extending from Guyana to Amapá, Brazil, do link consistently with those from south of the river, ranging from western Mato Grosso to easternmost Pará. As revealed by such morphometric examinations, the macrogeographic pattern of greater significance concerns eastern versus western Amazonian moieties rather than population segments on northern versus southern banks of the river. Illumination of barriers to gene exchange along this east–west versant may prove more decisive in resolving the morphological patterns and attendant taxonomic uncertainties we have uncovered.

THE PALMERA SAMPLE

Qualitative study of skins and skulls combined with results of multivariate analyses indicate that the 12 specimens from the Andean foothills in central Ecuador represent a population distinct from those samples we

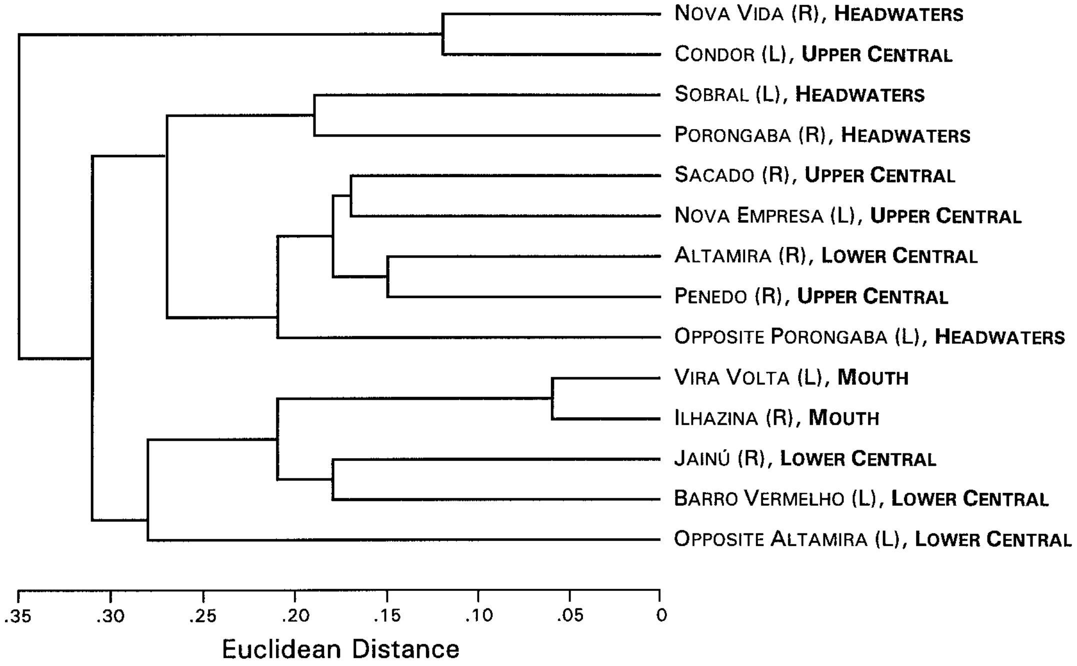

Fig. 43. UPGMA cluster diagram (using Euclidean distance measure) derived from log-transformed means for 14 samples of *O. megacephalus* collected on right and left banks along the Rio Juruá from the Headwaters Area downriver to the Upper Central Area, the Lower Central Area, and the Mouth Area. Samples are described in table 1; mean values for variables measured are listed in appendix A. See text for discussion.

identify as *Oryzomys yunganus.* We interpret the magnitude of the differences observed as that between two reproductively isolated entities; accordingly, the Palmera Sample should be designated as a new species.

Oryzomys tatei, new species

HOLOTYPE: AMNH 67361, an adult male captured by G.H.H. Tate (original number 2847) on February 9, 1924, at Palmera (01°25′S/78°12′W; locality 26 in gazetteer and map in figs. 14 and 47), at 4000 ft (1220 m), Provincia del Tungurahua, Ecuador. The specimen consists of a stuffed museum study skin with accompanying cranium and mandible (figs. 44, 45); all elements are intact and well preserved. External, cranial, and dental measurements are listed in table 22.

REFERRED SPECIMENS: Eleven others in addition to the holotype, collected along the upper Río Pastaza in central Ecuador at Palmera, 1220 m (AMNH 67358–67365, 67376); Mirador, 1524 m (locality 25; AMNH 67357), and Mera, 1160 m (locality 27; AMNH 67366, 67367). All were trapped by G.H.H. Tate from February 7 to March 3, 1924.

DIAGNOSIS: A member of the *Oryzomys yunganus* group characterized by its large body size, dark pelage, short and narrow incisive foramina relative to size of cranium, long toothrows, wide, robust molars, and blunt, triangular coronoid process (figs. 35, 44, 45, 46).

DESCRIPTION AND COMPARISONS: In traits associated with external dimensions and pelage coloration, examples of *Oryzomys tatei* resemble samples of *O. yunganus* (as we previously described that species), but differ in the following ways. *Oryzomys tatei* has, on average, larger lengths of head and body, and hind foot (table 21). Tone of upperparts of head and body is darker on average due to a greater concentration of melanistic hairs along the back and rump and the shorter and darker pigmented tips elsewhere on the body, particularly when contrasted with the brighter examples of *O. yunganus* in samples from Ecuador. Underparts are dark grayish white, again averaging slightly darker than the tone in most samples of *O. yunganus* (largely because of the relatively shorter unpigmented tips and longer segments of gray in the hairs). One specimen from Palmera (AMNH 67363) is partially melanistic; brownish black, silky fur extends from nose to rump along middorsal region of head and body, sides are brownish gray with a slight suffusion of buff; the venter is dark gray with a slight brown tinge. We have not seen a comparable melanistic example in any sample of *O. yunganus*. Examples of *O. tatei* have a thicker dorsal coat than do specimens of *O. yunganus*. Length of fur, as measured near the rump, ranges from 9 to 12 mm in the 12 specimens, which is greater than in samples of *O. yunganus* (see table 6). Variation of tail pigmentation in *O. tatei* parallels that seen in *O. yunganus*: the range extends from a monocolored brown tail to tails that are mottled on the ventral surface; in some specimens the tail is nearly bicolored along the proximal half (only slight touches of pigment). All specimens have six plantar pads, as is typical in samples of *O. yunganus* surveyed from western Amazonia (table 7); those on specimens from Palmera are much smaller relative to the thenar pads.

Oryzomys tatei shares a similar cranial conformation with *O. yunganus* (fig. 35), lacks a sphenofrontal foramen and squamosoalisphenoid groove, and resembles many samples of *O. yunganus* from western Amazonia in size of cranial dimensions (appendix C). Large crania are characteristic of these samples, but examples of *O. tatei* have relatively smaller incisive foramina with a longer bony palate and massive molars relative to cranial size. The toothrows are not only longer and the first upper molar wider relative to cranial size, but toothrows are longer and the first upper molar is wider in absolute values than in any sample of *O. yunganus*. Furthermore, the first upper molar is also wider relative to length of molar row than in any sample of *O. yunganus*. These contrasts can be appreciated in the descriptive statistics listed in appendix C and in re-

Fig. 44. Dorsal and ventral views of stuffed study skin of holotype of *Oryzomys tatei* (AMNH 67361). Measurements are listed in table 22.

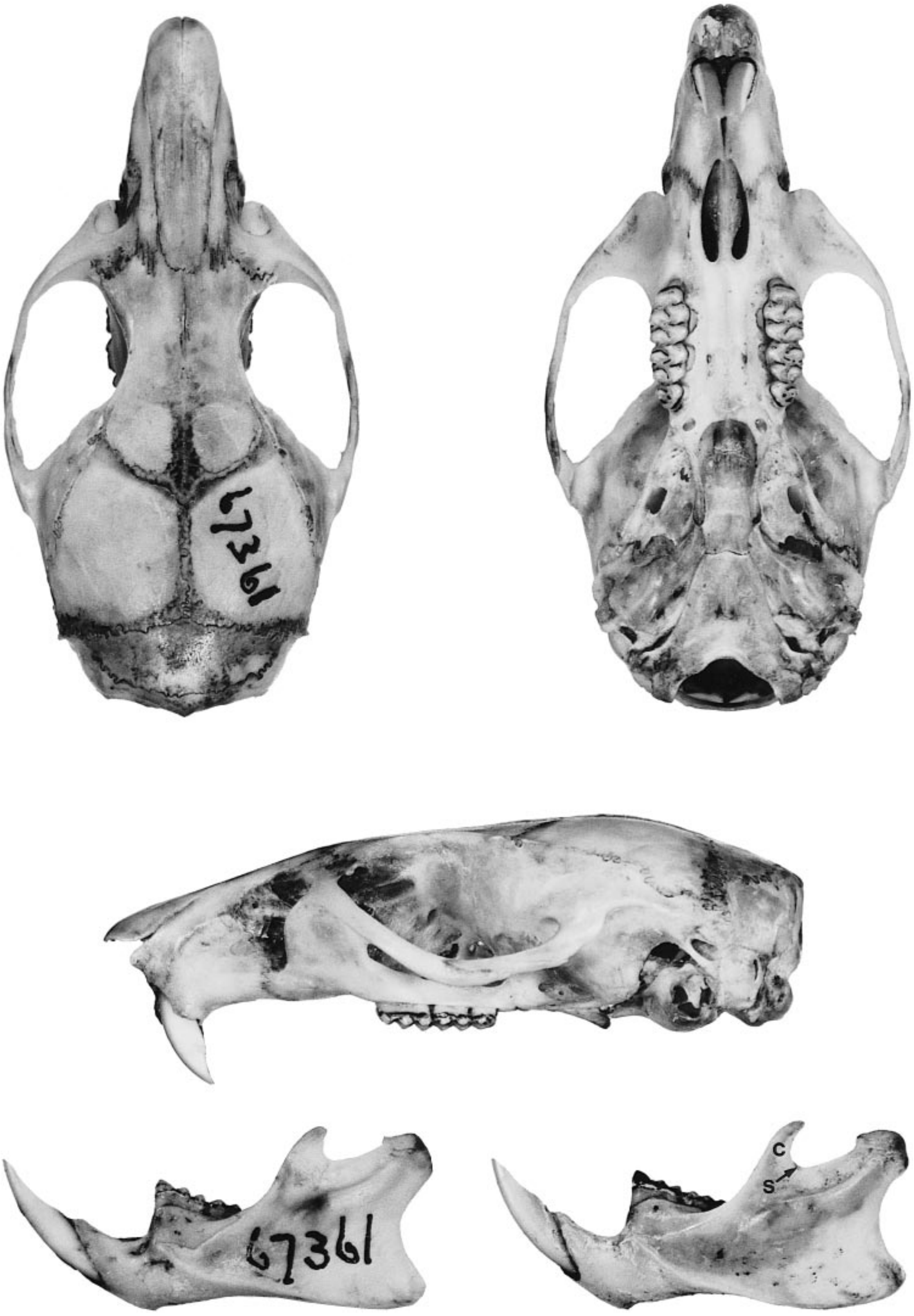

Fig. 45. Views of cranium and dentary of holotype of *Oryzomys tatei* (AMNH 67361). Measurements are listed in table 22. ×3. Dentary in lower righthand corner is from an Ecuadoran *O. yunganus* (AMNH 68106, locality 26 in gazetteer). Note its elongate coronoid process (**c**) and deep sigmoid notch (**s**) contrasted with the blunt process (which appears eroded but is intact) and shallower notch in *O. tatei*.

Fig. 46. Occlusal views of right upper and lower molars of *Oryzomys tatei* (AMNH 67357).

sults of principal components and discriminant function analyses (figs. 34, 36–39).

The dentary of *O. tatei* and *O. yunganus* is similar in overall shape, but differs in one detail (fig. 45). Compared with specimens of approximately equivalent age, *O. tatei* has a shorter and triangular (seen from the side) coronoid process with a shallow sigmoid notch (the concavity between coronoid and condyloid processes). The process has a blunt triangle compared with the coronoid extension in *O. yunganus*, which has a triangular base but a long and recurved tip, giving it a gracile configuration; a deep sigmoid notch is associated with the higher process in *O. yunganus*.

Aside from the striking difference in size of molars between the two species, occlusal patterns are similar. Each second upper molar of *O. tatei* has a short paraflexus, medial and labial fossettes (confluent in some specimens), and each second lower molar exhibits a fossettid and hypoflexid extending only halfway across the tooth (fig. 46; also see figs. 29–32).

DISTRIBUTION AND HABITAT: Known only from three localities in the Andean foothills between 1159 and 1524 m along the upper Río Pastaza in central Ecuador (figs. 14, 47).

On Cañadas's (1975) ecological map of Ecuador, Mirador, Palmera, and Mera fall within a continuous zone of Holdridge's (1967) ''Bosque Muy Humedo Premontano'' (= Premontane Very Humid Tropical Forest). This ecological zone is classified in the ''Perhumid'' Humidity Province, also in the sense of Holdridge. Mera appears to be at the western border of a vast, extremely wet ''Bosque Pluvial Premontano'' (= Premontane Tropical Rain Forest) zone of Holdridge's classification (see our discussion of the Holdridge classification in the account of *Oryzomys bolivaris*). The associated Humidity Province is ''Superhumid.'' All three sites are in a region receiving total annual rainfall exceeding 3000 mm (Haffer, 1987b). Tate's few observations about the localities were conveyed in letters to H. E. Anthony (in AMNH Mammalogy Archives) from which we extracted the following notes.

Mirador: Tate reached Mirador, the highest of the three localities, on February 1, 1924, by traveling below the Río Ulva and crossing the left bank of the Río Pastaza at Agoyan. A little below here are the ''famous falls,'' and it ''is from here the gorge of the river really begins and continues all the way down—some 200 feet deep.'' The vegetation showed ''sharp contrasts.'' In the gorge and along the road were a mixture of ''paramo or temperate plants'' with invaders from lower elevations. ''On the left the forest goes up without a break and every sheltered corner carries subtropical vegetation.''

Tate noted that the ''Pastaza valley is roughly a box cañon at the bottom of a V of hills. The side valleys come down steeply and the streams in them practically invariably form waterfalls into the cañon of the Pastaza. The intervening ridges between these valleys are high, the ends of them facing the Pastaza are generally a thousand feet

TABLE 21

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, and Hind Foot from Selected Samples in the *Oryzomys yunganus* group

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. Most samples contain the range in age from young to old adults. Sample numbers in parentheses refer to numbered collection localities in gazetteer. Specimens measured are identified in footnotes. We used only those specimens measured by field collectors whom we regard as careful in the way they obtain values.)

Species and sample	LHB	LT	LHF
Oryzomys yunganus			
GUIANAS AND EASTERN AMAZONIA			
FRENCH GUIANA[a]			
(5)	122.9 ± 7.92	107.0 ± 6.35	28.1 ± 0.84
	(113–139) 7	(101–120) 7	(27–29) 7
SURINAM[b]			
(10 + 11)	124.6 ± 7.37	102.7 ± 6.35	28.3 ± 0.84
	(110–133) 11	(90–115) 11	(27–30) 11
GUYANA[c]			
(12 + 13)	120.9 ± 6.40	116.8 ± 3.10	27.7 ± 1.11
	(112–132) 7	(114–121) 7	(26–29) 7
BRAZIL[d]			
(79 + 80)	115.0 ± 7.52	104.8 ± 6.40	28.8 ± 1.30
	(106–125) 5	(97–110) 4	(28–31) 5
(78)	107.0 ± 7.65	94.9 ± 4.04	26.7 ± 1.24
	(90–120) 18	(88–102) 18	(24–29) 18
TEPUIS AND WESTERN AMAZONIA			
VENEZUELA[e]			
(14)	126.5 ± 6.61	116.7 ± 5.78	28.3 ± 1.03
	(115–142) 15	(107–128) 15	(26–30) 15
PERÚ[f]			
(38)	115.0 ± 4.43	110.8 ± 6.43	28.2 ± 0.60
	(106–123) 11	(103–124) 11	(27–29) 11
(43 + 44 + 47)	117.8 ± 8.87	106.6 ± 11.04	27.7 ± 1.16
	(108–135) 10	(81–118) 10	(26–29) 10
(49)	117.0 ± 6.83	117.5 ± 9.40	30.3 ± 1.89
	(110–126) 4	(108–127) 4	(29–33) 4
BOLIVIA[g]			
(56 + 57)	112.6 ± 3.91	86.3 ± 4.50	27.2 ± 0.84
	(108–118) 5	(94–103) 4	(26–28) 5
(60)	126.0 ± 7.94	120.7 ± 4.04	27.7 ± 0.58
	(117–132) 3	(117–125) 3	(27–28) 3
BRAZIL[h]			
(67 + 69 + 70)	124.9 ± 6.82	108.0 ± 8.45	29.1 ± 2.28
	(113–136) 16	(89–120) 16	(25–33) 16
(68 + 71 + 73)	122.0 ± 6.01	104.5 ± 7.02	30.3 ± 1.77
	(112–136) 38	(93–120) 36	(27–37) 37
Oryzomys tatei			
ECUADOR[i]			
(25 + 26 + 27)	130.2 ± 6.31	112.3 ± 12.23	30.8 ± 0.87
	(118–137) 11	(89–127) 11	(30–32) 12

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[a] AMNH 266495, 266496, 266500, 266503, 266516, 266531, 257017.

[b] CM 76926–76931, 76933, 76936, 76937; FMNH 93284, 93286.

TABLE 21
(*Continued*)

[c] ROM 98719, 98738, 98747, 98771, 98782, 98824, 98826.

[d] **(79 + 80)**, USNM 521444, 521445, 521519, 521521, 521527; **(78)**, BMNH 81.518, 81.521, 81.523, 81.534–81.541, 81.543–81.547, 81.548, 81.593.

[e] AMNH 130896, 130898, 130899, 130901, 130905, 130906, 130914, 130916, 130933, 130940, 130955, 130959, 130960, 131125, 131126.

[f] **(38)**, BMNH 26.5.3.32–26.5.3.42; **(43 + 44 + 47)**, BMNH 28.5.1.9, 28.5.1.11, 28.5.1.13, 28.5.1.14; FMNH 24544, 24546–24549, 24551 **(49)**, LSUMZ 16685, 16687, 16689; MVZ 136585.

[g] **(56 + 57)**, AMNH 262736, 262950–262952, 262957; **(60)**, AMNH 262079, 262081; MSB 56001.

[h] **(67 + 69 + 70)**, JLP 15257, 15415, 15446, 15523, 15535, 15605, 15720; JUR 2, 8, 35, 37, 38, 46, 75, 110; MNFS 527, 918; **(68 + 71 + 73)**, JLP 15262, 15263, 15265, 15275, 15281, 15283, 15288, 15289, 15312, 15319, 15321, 15324–15329, 15361, 15476, 15495, 15519, 15759, 16021, 16068; MNFS 335, 341, 349, 368, 384, 387, 388, 391, 392, 412, 511, 519, 521, 697.

[i] AMNH 67357–67367, 67376.

above the river and as they run back they rise continually higher.''

``Mirador is well-named,'' wrote Tate. ``I can see Palmera, my next camp. Ten miles away. We are about 15 miles E of Baños.'' Tate's barometer was unreliable, so he had to depend on the elevation as given by a railroad survey map: ``5110 feet. I shall call it 5000.'' Weather conditions at Mirador were frequently rainy, cold, and windy, especially at night.

Palmera: ``The weather at this locality,'' Tate wrote Anthony, ``seems to be generally milder than at Mirador. Still, there is rain and fog. . . . This is a monthly weather summary given me by the owner of this hacienda who has lived here 3 years and kept a rain chart. I believe it is about right:—Jan. rainy, Feb. quite dry, Mar. dry, April very rainy, May indifferent, Jun. dry, Aug. rainy, Sept. rainy, Oct. dry, Nov. very dry, Dec. dry.'' Brown (1941) commented that local conditions at Palmera are about the same as at the Río Topo, which ``is an extremely wet region, probably the rainiest in the foothills along the Pastaza'' (p. 850).

Mera: Tate moved camp from Palmera to Mera on February 25 (fig. 48). ``Mera itself although high above the river is really out in the flat country. A few ridges persist, but are only truly noticeable when one is climbing up them. The country is pretty boggy here and every other step one sinks over one's ankle. . . . Almost entirely composed of bog, nothing to eat and nothing to collect as far as I can see.'' Tate noted that the ``day temperature averages 70°. This is comparatively cool so I think we can scarcely consider Mera as in the tropics—subtropics about fits I think.'' He also mentioned that the vegetation is dense. It was very rainy at Mera; Tate joked that ``Mera is afloat—almost.'' Brown (1941: 836) noted that at Mera, the ``mean annual temperature is about 21° C. with a maximum of 27° and a minimum of 16° C. The average annual rainfall is over 4500 mm. In 1932 it was 6010 mm. The wettest months are between March and August. During the dry season the average monthly rainfall amounts to as much as 250 mm.''

Unfortunately, Tate did not describe the habitat in which he actually caught the rats; at least we could not locate such information in letters or field journals.

In 1975, when A. L. Gardner worked in the Palmera region, patches of forest remained; it was Gardner's impression that the extent of deforestation had not changed much since Tate's visit in 1924. Rageot and Albuja (1994) described the Mera area as a patchwork of cultivated land, second-growth forest, and primary forest (their survey extended from 1981 to 1993).

SYMPATRY: No other species in the former *O.* ``*capito*'' group is represented by specimens from Mirador, Palmera, or Mera. Examples of other sigmodontines, however, have been collected at the same sites where *O. tatei* was encountered: *O. auriventer* from Mirador (the holotype, BMNH 99.9.9.25), Palmera (AMNH 67340–67347, 67398, 67433), and Mera (AMNH 67348–67351); *O. balneator* from Mirador (AMNH 67571; the holotype, BMNH 99.9.9.34); *Chilomys*

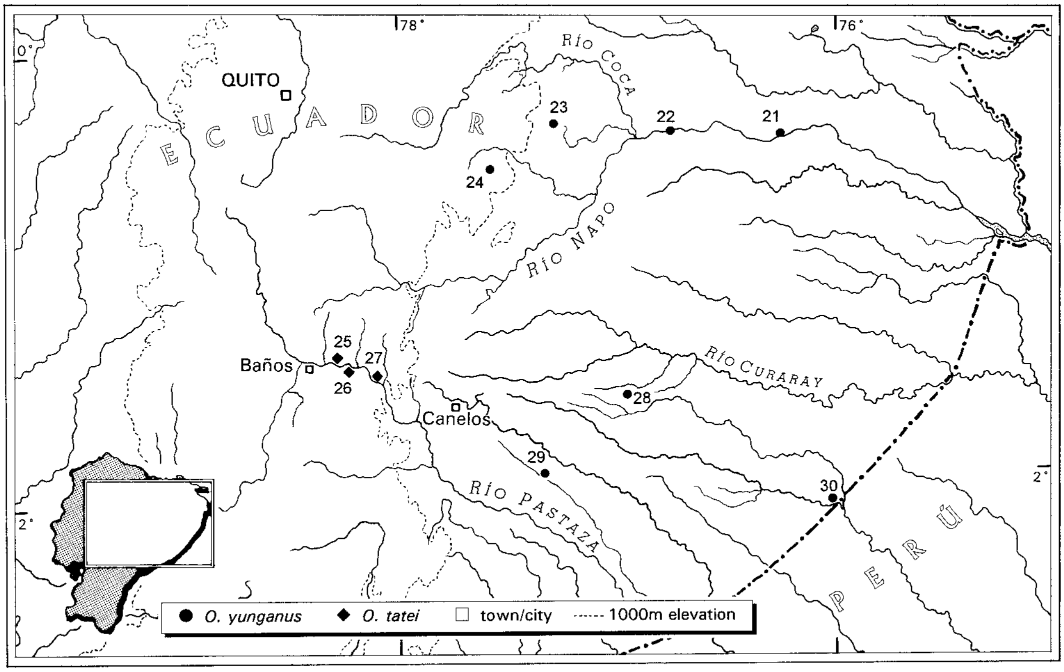

Fig. 47. Distribution of collection localities for *Oryzomys tatei* (Mirador, locality 25; Palmera, locality 26; and Mera, locality 27) and *O. yunganus* (localities 21–24 and 28–30, which are identified in gazetteer) in central and northern Ecuador.

instans from Mirador (AMNH 67544, 67545, 67574) and Palmera (AMNH 67546, 67547); and *Scolomys melanops* from Mera (AMNH 67518, 67520–67523, and the holotype, 67524); *Akodon aerosus* from Mirador (the holotype, BMNH 99.9.9.105; AMNH 67573, 67728), Palmera (AMNH 67426, 67427, 67458, 67459, 67461), and Mera (AMNH 67428–67431, 67462–67466, 67473; and *Neacomys spinosus* (AMNH 67519, 67525, 67526, 67567) from Mera. Specimens in the American Museum were all collected by G.H.H. Tate during February and March 1924, the same period when he trapped the examples of *O. tatei.*

Rageot and Albuja (1994) reported results of a mammal survey undertaken in the Mera region during a period of 10 years. Sigmodontine rodents formed only a skimpy portion of the 1044 specimens captured (collecting bats was the obvious priority), but among these is a specimen of *Oryzomys auriventer* (USNM 548370) from a site 4 km northeast of Mera, a series of *Oligoryzomys destructor* (USNM 548372–548379; they referred to it as “*longicaudatus*“), an example of *Oecomys bicolor* captured 4 km northeast of Mera, *Neacomys spinosus* (USNM 548380), and specimens of *Nectomys squamipes* (USNM 548371, 548385–548391), *Akodon aerosus* (USNM 548382–548384), and *Scolomys melanops* (USNM 399936, 399937, 548381).

Rageot and Albuja (1994: 194) also recorded five specimens of “*Oryzomys capito*” captured in primary forest. We have not seen this series, which they described as having bicolored tails shorter than length of head and body, dark upperparts, and grayish white underparts. The series should be reexamined to determine if all or some of the specimens are examples of *O. tatei.*

REMARKS: The combination of diagnostic traits for *Oryzomys tatei* is not found in any other sample from Ecuador. Specimens from Llunchi (locality 22), San José Abajo (locality 23), and Río Tigre (locality 30) that form our population sample 6 (Napo + E Pastaza) in table 16 are similar to specimens of *O. tatei* in overall cranial size (see appendix C),

Fig. 48. The village of Mera with forest in the background, Provincia de Pastaza, central Ecuador (locality 27 in gazetteer; fig. 47). Photographed by G.H.H. Tate, who worked at Mera during the last week in February and the first week in March 1924.

but have larger incisive foramina and much smaller molars. We measured only toothrows and molar breadths of the four specimens from the ríos Yana Rumi and Capahuari (localities 28 and 29, respectively), places closest to the Palmera region from which we have samples of *O. yunganus*; 5.2–5.3 mm is the range for length of molar row, and 1.5–1.6 mm the range for breadth of first upper molar, values that fall within ranges given for population sample 6. Our only other samples from the Andean foothills in Ecuador consist of eight specimens from San Francisco Aguarico in the northern part of the country (locality 21) and Zamora in the south (locality 31). Only toothrows were measured for these specimens, and the range in values is comparable to that seen in the other samples of *O. yunganus* from Ecuador (CLM1–3 = 4.9–5.3 mm and BM1 = 1.5 mm in the sample of eight; CLM1–3 = 4.7 mm and BM1 = 1.6 mm in the Zamora individual). No other sample collected in the Andean foothills, from Colombia to Bolivia, no matter what the elevation, exhibits the combination of traits we regard as diagnostic for *O. tatei*.

Three of the species that Tate obtained from Mirador, Palmera, and Mera have been encountered only in wet and cool premontane evergreen forests along the Andean foothills from Venezuela to Perú. *Oryzomys auriventer*, a member of the *O. albigularis* group that has distinctive morphological (Thomas, 1899) and chromosomal (Gardner and Patton, 1976) traits, was captured in the Palmera region and has also been collected in the premontane foothill rain forest of southern Perú in Departamento de Ayacucho at Huanhuachayo, 1660 m (LSUMZ 16667–16669). *Oryzomys balneator* is small-bodied, long-tailed, and morphologically distinct compared to any of the other species now included in *Oryzomys*. It was known only by the type series from Mera (Thomas, 1900)

TABLE 22
Measurements (mm) of Holotypes for Species in the *Oryzomys yunganus* Group

	O. yunganus BMNH 2.1.1.39	*O. tatei* AMNH 67361
Age	Old adult	Adult
Sex	Male	Male
LHB	125	133
LT	128	121
LHF	28	31
LE	21	—
ONL	31.3	33.0
ZB	16.6	16.9
IB	4.9	5.2
LR	10.2	10.2
BR	6.2	6.0
LB	12.1	12.5
HBC	8.8	8.3
BZP	3.5	4.2
LD	7.8	8.1
LBP	6.4	7.4
PPL	10.8	10.8
LIF	5.1	4.6
BIF	2.2	2.1
CLM1–3	4.8	5.7
BM1	1.5	1.8

until Anthony (1924: 139) described *O. b. hesperus,* which is based on specimens in AMNH “taken only in the Western Andes of southern Ecuador, and in the Cordillera de Chilla, a spur of this range.” Whether on the lower east or west flanks of the Ecuadoran Andes, *O. balneator* has only been found in a zone of wet and cool forest habitats. *Chilomys instans* is also found in this forest band, but has a broader distribution extending from the Táchira and Mérida Andes in western Venezuela (Handley, 1976) south through the Cordillera Oriental in Colombia (Thomas, 1895) to central Ecuador (specimens in AMNH). It also has a greater elevational range; specimens from central and northern Ecuador in the American Museum collection were taken between 1220 m at Palmera to 3399 m at San Ignacio on the slopes of Volcán Pichincha. The morphologically distinctive *Akodon aerosus* (Thomas, 1913), according to Patton and Smith (1992: 88) ranges “from Ecuador to central Bolivia” and “is narrowly confined to the upper montane forests of the eastern Andean slopes between about 2000 and 1200 m.”

Oryzomys tatei may also be a component of this wet and cool premontane forest fauna and should be sought in similar habitats elsewhere along the eastern flanks of the Andes in Ecuador as well as Perú.

Other species recorded from the Mera region, where *O. tatei* was encountered, are either spread over a wide elevational gradient or are basically elements of lowland tropical evergreen rain forest that happen to occur as high as Mera. *Oligoryzomys destructor* occurs in an altitudinal belt between 600 and 3350 m on the eastern flanks of the Ecuadoran Andes (Carleton and Musser, 1989). *Scolomys melanops* is known by the specimens from Mera and has also been collected at Huamaní on Volcán Sumaco in Provincia de Napo and in the Amazonia lowlands of northern Ecuador at Limóncocha, 250 m (Patton and da Silva, 1995). Furthermore, *Oecomys bicolor, Neacomys spinosus, Nectomys squamipes,* and *Rhipidomys leucodactylus* extend from the elevation at Mera down to lowlands of the Amazon Basin (Hershkovitz, 1944; Voss and Emmons, 1996; Musser et al., unpubl.; Tribe, 1996).

ETYMOLOGY: It is a pleasure to acknowledge George H. H. Tate (fig. 49) for his diligent survey efforts in South America that resulted in large collections of small mammals, particularly rodents, from Ecuador, Bolivia, and Venezuela. These specimens remain at the foundation of any inquiry into systematics of Neotropical mammals.

SUMMARY

We consider the intersample variability uncovered by our observations of skins and skulls, as well as multivariate analyses, to represent two species. *Oryzomys tatei* is documented only from wet rain forests at the western margin of the Amazon Basin in central Ecuador. It is morphologically similar to *O. yunganus,* but is clearly distinguished from that species by a set of external, cranial, and dental traits. The geographic range of *O. tatei* is apparently confined to a region characterized by the distributions of three other taxa of sigmodontines.

Qualitative and multivariate analyses of all other samples suggest geographic variation

Fig. 49. George H. H. Tate at camp on Cerro Duida, Venezuela (1928).

within one species occurring throughout Amazonia—*O. yunganus.* This definition of *O. yunganus* is a provisional hypothesis that must be tested before accepting another explanation of the variation in cranial size, frequency of occurrence of the hypothenar pad, and chromosomal traits evident among the samples. More specimens need to be obtained and analyzed from geographic areas unsampled by us, particularly the central Amazon Basin; our geographic coverage is dense only in the Guiana Region and along the western margin of the basin. Also necessary are surveys along the transects we defined, as well as others, to better resolve the distribution of variation in body size and its significance in determining whether it is representative of one or more species. Our intent in this report is to identify all specimens that demonstrate the morphological traits associated with the holotype of *O. yunganus.* To us, *O. yunganus* is characterized by a distinctive combination of external, cranial, dental, and chromosomal traits. It occurs in parts of its geographic range with *O. megacephalus, O. nitidus,* and *O. macconnelli,* and possibly with *O. talamancae.* The five species can be distinguished from one another by a suite of morphometric characters, differences in coloration and texture of pelage, and chromosomal variation. Moreover, morphological patterns of the carotid circulatory system and occlusal surface of second upper molars, when taken in combination, unambiguously set *O. yunganus* apart not only from *O. megacephalus, O. nitidus,* and *O. macconnelli,* but also from others that had at one time been lumped with *O. yunganus* into one species (Tate, 1939; Hershkovitz, 1960; Cabrera, 1961); that is, *O. laticeps, O. talamancae, O. bolivaris,* and *O. alfaroi* (fig. 151; table 52).

Oryzomys tatei inhabits wet evergreen rain forest on the western rim of the Amazon Basin in central Ecuador; *O. yunganus* is indigenous to tropical evergreen rain forests of the

Amazon Basin, Guiana Region, and tepuis in eastern Venezuela. These regions are included in the broader Amazonia (Haffer, 1987a: 111). Among members of the former *O.* ''*capito*'' complex, the range of *Oryzomys macconnelli* and bulk of the distribution of *O. megacephalus* are also Amazonian. By contrast, the next two species we treat are found in northwestern South America and Central America—the trans-Andean region.

THE TRANS-ANDEAN SPECIES, *ORYZOMYS BOLIVARIS* AND *ORYZOMYS TALAMANCAE*

The trans-Andean forest region, as outlined by Haffer (1987a: 123), ''comprises the humid lowlands west and north of the Andes, i.e. the Pacific rain forests of Colombia and Ecuador, the humid portions of Caribbean Colombia, the humid middle Magdalena Valley and the forested lowlands of Middle America.'' *Oryzomys bolivaris* and *O. talamancae* are the only species in the former *O.* ''*capito*'' complex that occur in this part of the Neotropics. Their accounts follow.

ORYZOMYS BOLIVARIS Allen, 1901

In the checklist of *Mammal Species of the World,* Musser and Carleton (1993: 720) used *bolivaris* (Allen, 1901) as the oldest name available for the species formerly recognized as *Oryzomys bombycinus*. We document that identity here. Originally described by Goldman in 1912, characteristics of *O. bombycinus* were more fully elucidated by him in 1918. Goldman (1918: 76) indicated that the species occurs in ''heavily forested areas from southern Costa Rica to eastern Panama, and probably western Colombia; altitudinal range from sea level to at least 3,000 feet.'' Goldman studied only eight specimens, all from Costa Rica and Panamá, but thought the morphological variation of the samples reflected two recognizable populations, typical *O. bombycinus* from Panamá and *O. b. alleni* from Costa Rica. Although the southern extent of the species was unknown, Goldman (1918: 77) speculated that the two subspecies ''may not improbably prove to be geographic races of *O. nitidus* of Perú, since Ecuadoran specimens believed to be near *nitidus* show close alliance to the North American forms.'' Goldman's delimitation of *O. bombycinus* was referenced by himself and other authors producing regional faunal studies during the subsequent decades (Goldman, 1920; Goodwin, 1946; Handley, 1966).

Pine (1971) expanded the morphological and geographic components of *O. bombycinus* and documented samples collected after Goldman's monograph. In contrast to Goldman's meager sample, Pine was able to assemble 57 specimens from Central America and northwestern South America. He interpreted the morphological variation in the samples to represent three geographic units: *O. b. bombycinus* from central Panamá; *O. b. alleni,* occurring in Nicaragua, Costa Rica, and western Panamá; and *O. b. orinus,* a name originally used to set apart samples from eastern Panamá (Pearson, 1939) but now applied also to specimens from western Colombia and northwestern Ecuador. Pine's definition of *O. bombycinus* has been the standard reference for subsequent literature on the species, including reports that have varied from geographic extension (Benshoof et al., 1984) to regional faunal studies (Hall, 1981; Jones and Engstrom, 1986; Timm et al., 1989).

We have studied 104 specimens, which include the six holotypes bearing the scientific names we associate with the species. In addition to *bombycinus, alleni,* and *orinus,* whose association as one species has never been questioned (Pine, 1971), we discovered that *bolivaris, castaneus,* and *rivularis,* all described by Allen (1901), are based on specimens that also represent this same species. Gardner and Patton (1976: 40) had already suggested that the holotype of *rivularis* is an example of what Pine called *O. bombycinus.*

The identity of these six names with one species, *O. bolivaris* Allen (1901), is documented later in the Taxonomic Summary. In this account, we provide a gazetteer of collecting localities for specimens we examined and discuss the significance of the distribution spanned by those localities within the context of vegetational and climatic zones. Morphology of *O. bolivaris* is then described, followed by qualitative and quantitative comparisons with *O. talamancae* and *O. alfaroi*, two morphologically similar species that occur in the same region. We analyze character variation among samples of *O. bolivaris* and discuss its implication for recognizing subspecies. These parts combine to substantially alter the species definition outlined by Pine (1971).

GAZETTEER AND SPECIMENS

Collection localities for the 104 specimens of *O. bolivaris* we studied are listed below. The number preceding each locality keys to a symbol on the map in figure 50. We have not listed any specimens not personally examined.

HONDURAS

Departamento de Gracias a Dios

1. **Río Mairin Tingni** (Río Plátano Biosphere Reserve), ''approximately ½ kilometer up river from where it empties into the Río Plátano'' (Benshoof et al., 1984: 511), 15°38′N/84°55′W, 50 m: MSB 45820, 45823, 45825–45827.

NICARAGUA

Provincia de Zelaya

2. **Río Kurinwas** (campsite), 12°52′N/84°05′W (from Pine, 1971: 592), 10 m: USNM 392860. **within** ½ mi of former locality, 10–25 m: USNM 392681, 392682. **5.5 mi downstream from campsite,** below 10 m: USNM 392863.
3. **Bluefields, 0.8 km W Water Pumping Station on road to El Pool**, ca. 12°00′N/83°45′W: MVZ 140659.

COSTA RICA

Provincia de Alajuela

4. **Cantón de Upala, Distrito Dos Ríos, 1.7 km S Finca Jirón, S of Río Pizote,** 10°51′N/85°10′W (for Upala), 400–420 m: NW 325.
5. **Monteverde Cloud Forest Preserve, La Esperanza,** 15 km W Tigre, Río Peñas Blancas, in foothills of the Cordillera de Tilarán (see Reid and Langtimm, 1993), 10°19′N/84°43′W, 800 m: KU 143312.
6. **Villa Quesada** (''The largest town on the northwest slopes of Cerro Platanar on Highway 15,'' McPherson, 1985: 271), 10°19′N/84°26′W, 2000 ft: FMNH 44005. **Seven km by road NE Villa Quesada**, 700 m: LSUMZ 26352, 26356.

Provincia de Heredia

7. **La Selva Biological Station** (''Finca La Selva'' on specimen tags)**, 3 km S Puerto Viejo** (see maps and discussion in Slud, 1960; Timm et al., 1989; Hartshorn, 1983: 136; McDade et al., 1994), 10°27′N/84°00′W, 30 m: UMMZ 125187, 125188.
8. **Parque Nacional Braulio Carrillo, 11 km S, 4.5 km W Puerto Viejo** (see map and description in Timm et al., 1989), 10°22′N/84°03′W, 325 and 680 m: FMNH 128490–128493.
9. **8 km N, 27 km W Guápiles** (which is ''A railroad town 12 km W of Guácimo . . . 250–350 m,'' McPherson, 1985: 258),10°13′N/83°47′W (for Guápiles, USBGN Costa Rica, 1983: 47): KU 143314.

Provincia de Limón

10. **Cariari, on the Río Tortuguero** (Cariari is ''an Instituto de Tierras y Colonización [ITCO] colony north of Guapiles,'' Gardner and Patton, 1976: 42), 10°22′N/83°31′W, 100 m: LSUMZ 13171–13175, 15326.
11. **Guápiles** (see locality 9), 10°13′N/83°46′W, 240 m: CM 1326.

Provincia de Cartago

12. **Tuis,** ''about 11 km. southeast of Turrialba'' (Selander and Vaurie, 1962: 63; ''a small pueblo 13 km SE of Turrialba,'' ''9°59′ × 83°34′,'' according to McPherson, 1985: 270), 09°51′N/83°35′W, 2250 m: AMNH 9622/7962, 9624/7964, 9631/7971 (holotype of *Oryzomys nitidus alleni*).

Provincia de Puntarenas

13. **7.8 km SW San Vito de Java** (''San Vito'' in USBGN Costa Rica, 1983: 114; ''a small town W of the Panamanian Border near Cañas Gordas and about 20 km N of the Pan American Highway at Villa Neily,'' McPherson, 1985: 269), 08°50′N/82°58′W (for San Vito, USBGN Costa Rica, 1983: 114), 1350–1450 m (McPherson, 1985: 269): MSU 14531.

PANAMÁ

(Unless indicated otherwise, coordinates are from Fairchild and Handley, 1966.)

Provincia de Bocas del Toro

14. **Río Changena,** 09°06′N/82°34′W, 2500 and 2600 ft: USNM 319475–319478.

Provincia de Chiriquí

15. **Bugaba** (= Bogavo), 08°29′N/82°37′W, 250 m: BMNH 0.7.11.47.

Provincia de Coclé

16. **El Valle,** 08°36′N/80°08′W, 2000–3000 ft: USNM 304809.
17. **6 mi E El Valle**: USNM 304810.

Provincia de Colón

18. **Cerro Bruja,** 09°29′N/79°34′W, 1000 ft: USNM 171529.

Provincia de Panamá

19. **“Cerro Azul,”** the name on skin labels of specimens collected by either Goldman or Handley; it actually refers to two places (see Fairchild and Handley, 1966: 18–19): **Cerro Prominente,** 09°13′N/79°18′W, 2500–3000 ft, which is the ‘‘Cerro Azul’’ of E. A. Goldman, USNM 171103, 171104, 171105 (holotype of *Oryzomys bombycinus*); **La Zumbadora,** 09°14′N/79°21′W, 2000–3000 ft, which is the ‘‘Cerro Azul’’ of C. O. Handley, Jr., USNM 305647–305658, 306916–306925, 305704 (incorrectly identified as *O. talamancae* by Musser and Williams, 1985: 11), 305705.
20. **Pacora (¼** mi S Altos de Pacora), 09°04′N/79°18′W, 2300 ft: MSU 20540.

Provincia de Darién

21. **Loma Cana,** a ridge near Mount Pirre (Pearson, 1939: 3), 4900 ft: ANSP 19705, 19707.
22. **Mount Pirre,** ‘‘along the Río Limón’’ (Pearson, 1939: 2), 07°51′N/77°44′W, 4700 ft: ANSP 19708, 19709 (holotype of *Oryzomys bombycinus orinus*). **Darién World Heritage Site** (formerly Darién National Park): USNM 565921 (trail from Rancho Frio Station to ‘‘Rancho Frio 2,’’ 790 m), 565922, 565923 (Mount Pirre Range, ‘‘Rancho Plastico,’’ above Pirre INRENARE Station, 1150 m).
23. **Cerro Tacarcuna** (this is the ‘‘Cerro Tacarcuna’’ listed in Fairchild and Handley, 1966: 17, who note that the ‘‘Mount Tacarcuna’’ referred to by Anthony [1916] and Goldman [1920] is actually Cerro Malí, 08°07′N/77°14′W), 08°10′N/77°18′W, 4000 ft: USNM 338260.

COLOMBIA

Departamento del Chocó

24. **Condoto,** ‘‘southern Chocó close to western base of central Western Andes near mouth of Río Condoto’’ (Paynter and Traylor, 1981: 59), 05°06′N/76°37′W, 300 and 450 ft: BMNH 13.8.10.6, 13.8.10.7, 14.5.28.13, 14.5.28.14.

Departamento del Valle del Cauca

25. **6 mi N Buenaventura,** Buenaventura being a ‘‘major port on Pacific, across Bahía de Buenaventura from mouth of Río Dagua’’ (Paynter and Traylor, 1981: 27), 03°53′N/77°04′W, 40–60 m: USNM 554232, 554235, 554236.
26. **Río Raposo, Virology Field Station, 27 km S Buenaventura,** 03°38′N/77°05′W: USNM 334698.

Departamento del Cauca

27. **Río Mechenque** (see Paynter and Traylor, 1981: 158), 02°40′N/77°12′W, 800 m: FMNH 90215.

Departamento de Nariño

28. **Barbacoas,** on ‘‘Pacific coastal plain, close to western foothills of Western Andes, on Río Telembí, an affluent of Río Patía’’ (Paynter and Traylor, 1981: 17; see the map in Allen, 1916a), 01°41′N/78°09′W, 23 m: AMNH 34219 (misidentified as *O. talamancae* by Musser and Williams, 1985: 12).

ECUADOR

Provincia de Esmeraldas

29. **Carondelet,** ‘‘on coastal plain on Río Bogotá, northern Esmeraldas’’ (Paynter, 1993:32), 01°06′N/78°45′W, 60 ft: USNM 113293, 113294.
30. **San Javier**, ‘‘interior northern Esmeraldas on coastal plain, on railway, near where Río Cachabí swings abruptly W, 13 km E of Maldonado’’ (Paynter, 1993: 183), 01°04′N/78°47′W, 60 ft: USNM 113292, 113296, 113297; BMNH 1.3.19.11 (holotype of *Oryzomys castaneus*).

Provincia del Pichincha

31. **Río Verde,** 3200 ft, a ‘‘river merging with Río Guaillabamba [00°28′N/79°25′W] at W base of Catacache hills;’’ see Paynter and Traylor (1977: 130), who explained that this river in Provincia Pichincha is not the Río Verde at 01°04′N/79°25′W in Provincia Esmeraldas because the latter flows from the central Esmeraldas coastal plain, maximum altitude 300 m, to the ‘‘town of Rioverde’’ on the coast at 01°04′N/79°25′W: BMNH 1.1.6.6 (holotype of *Oryzomys rivularis*).
32. **1 km (by trail) N Mindo**, 00°02′S/78°48′W (for Mindo, Paynter, 1993: 126), 4960 ft (R. S. Voss, field notes; copy in Voss’s personal files at AMNH): UMMZ 155824–155826.
33. **Gualea, Río Tulipe** (see Paynter and Traylor, 1977: 126), 00°05′S/78°47′W, 1200 m: FMNH 94970.
34. **Santo Domingo de los Colorados** (Paynter and Traylor, 1977: 116), 00°15′S/79°09′W, 1600 ft: BMNH 15.1.1.41, 15.1.1.42.

Provincia de Manabí

35. **[Cerro of] Pata de Pájaro** (Chapman, 1926: 715), 00°02′N/79°59′W (for nearby village of Pata de Pájaro, which is ‘‘near base at western side of Montañas de Chindul, ca. 18 km inland, northern Manabí,’’ Paynter, 1993: 150; also, see Foster, 1992: 29), 700 ft (camp at base of Cerro, G.H.H. Tate, field notes, AMNH Mammalogy Archives): AMNH 66234, 66235 (both misidentified as *O. talamancae* by Musser and Williams, 1985), 66238.

Provincia de Bolívar

36. **Hacienda Porvenir** (location of this place is discussed in Taxonomic Summary), 1800 m: BMNH 99.9.9.27 (holotype of *Oryzomys bolivaris*).

DISTRIBUTION OF *ORYZOMYS BOLIVARIS* and Associated Vegetational, Climatic, and Habitat Generalities

Our confirmed records of *Oryzomys bolivaris* describe a geographical range from northeastern Honduras (about latitude 16°N) through eastern Nicaragua, Costa Rica, Panamá, and western Colombia to west-central Ecuador (about latitude 1°S), and an elevational belt from slightly above sea level to 1494 m (Mt. Pirre area, Panamá) and 1800 m (Hacienda Porvenir, Ecuador).[4] This distribution generally conforms to a relatively narrow band of very wet and permanently humid forest (see map in fig. 50) known as the trans-Andean forest region (Haffer, 1967). It includes, as Haffer (1987a: 111) explained, ''the Pacific lowlands of northwestern Ecuador and Colombia, portions of the Caribbean lowlands of Colombia, as well as the lowlands of Middle America (mainly along the Caribbean slope).''

Prevailing trade winds from the northeast pick up moisture as they blow over the Atlantic Ocean and Caribbean Sea, and subsequently release it onto Middle and South America. ''Rains fall where the movement of the tropical air masses is slowed, e.g., on the windward side of a barrier such as a hilly region or a mountain range. Therefore, the windward (eastern) slopes of the mountains from Mexico through northern South America to Brazil have a humid climate'' (Haffer 1987b: 3).

An explanation of the climatologic forces responsible for the South American component of the trans-Andean forest region is provided by Trewartha (1961:15): ''Although an easterly circulation [of air flow] is characteristic of most of the eastern equatorial Pacific, in the easternmost part, in the vicinity of northwestern Ecuador and western Colombia, there exists a circulation which is prevailingly from the west and consequently onshore.'' Trewartha is unclear what factors induce the unexpected onshore winds, but he cites the postulations of other researchers, mostly H. Flohn's, regarding a local fragment of a global system of equatorial westerlies that create '' 'monsoons' whose convergent character, general instability, and deep humidification cause them to be ripe for abundant shower activity. . . . Having had a recent trajectory over very warm waters, when these unstable onshore westerlies are forced upward along the flanks of the Colombian Andes, heavy showery rains are the result'' (Trewartha, 1961: 15).

Trewartha (1961) also expounded upon the peculiar northward displacement of the tropical climates from their expected latitudes on the Pacific coast, documenting in passing the astounding rainfall statistics that typify parts of Ecuador and especially the Chocó of Colombia, considered by many to be the wettest region on the planet (Gentry, 1982). Additionally, he mentions the anomalous latitudinal expanse of dry areas in northern Chile and Perú, as well as central and southern coastal Ecuador, and the nature of the narrow transition belt between the wet and dry climates there.

When comparing the distribution of collecting localities of *Oryzomys bolivaris* with even the crudest ecological maps, it is apparent that the species lives in very wet and floristically rich regions. But to quantify the wetness, vegetational diversity, as well as physiographic and climatic distinctions of its habitat with a single and straightforward description proved to be frustratingly elusive; no adequate answer is available. A variety of terrestrial ecosystem classifications exist that are based on climatic, vegetational, and topographic syntheses (for some examples, see Holdridge et al., 1971; Köppen, 1931; Lauer, 1959; and Troll, 1966), but no system presents a complete and accurate depiction.

Several schemes deserve mention. The life-zone pyramid devised by Holdridge combines information reflecting the interplay of latitude, altitude, biotemperature (Holdridge's term; Holdridge et al., 1971), annual precipitation, and potential evapotranspira-

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[4] McPherson (1985, 1986) identified *Oryzomys bolivaris* (he used the name *bombycinus*) as endemic to the wet forests of Costa Rica and Panamá. Pine's (1971) review documented specimens from Nicaragua, Colombia, and Ecuador and had clearly indicated a more expansive range for the species.

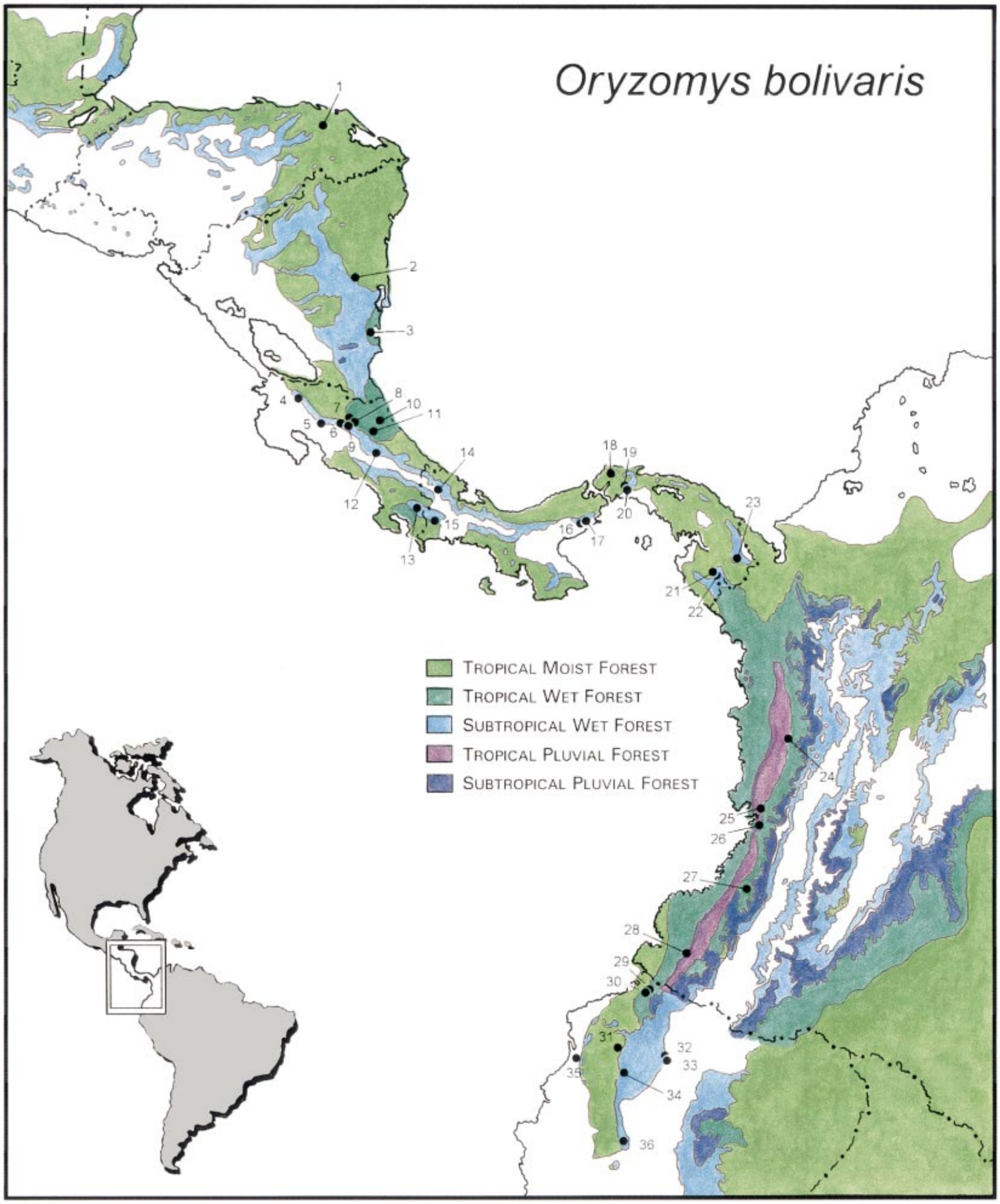

Fig. 50. Distribution of *Oryzomys bolivaris* (based on collection localities for 104 specimens examined) and its relationship to forest formations (indicated by Holdridge's [1967] scheme of life zones) in the trans-Andean region. Numbers key to localities in the gazetteer for *O. bolivaris* where locality information is provided, and specimens are identified by museum initials and catalog numbers. The correspondence between localities and Holdridge's life zones and humidity provinces is summarized in table 23. Holdridge life zones are in color. SUBTROPICAL WET FOREST includes PREMONTANE and LOWER MONTANE; SUBTROPICAL PLUVIAL FOREST includes PREMONTANE and LOWER MONTANE.

TABLE 23

Correspondence between Collection Localities for *Oryzomys bolivaris* and Holdridge's Life Zones and Humidity Provinces in the Trans-Andean Region

(We first constructed a map showing the distribution of collection localities, ignoring any reference to vegetative zones. On a separate layout we outlined Holdridge's zones [slightly modified as explained in the footnote below] on a map of the trans-Andean region. Finally, we overlaid the distribution of life zones with the map of localities. Habitat information from skin labels or field journals as well as published ecological descriptions available for certain locations provided a control of the match between plot and zone. See map and legend in fig. 50 and discussion in text.)

Country and numbered gazetteer locality	Holdridge System	
	Life Zone[a]	Humidity Province
HONDURAS		
1	Tropical Moist Forest	Humid
NICARAGUA		
2	Tropical Moist Forest	Humid
3	Tropical Wet Forest	Perhumid
COSTA RICA		
4	Subtropical Wet Forest	Perhumid
5	Subtropical Wet Forest	Perhumid
6	Subtropical Wet Forest	Perhumid
7	Tropical Wet Forest	Perhumid
8	Tropical Wet Forest	Perhumid
9	Subtropical Wet Forest	Perhumid
10	Tropical Wet Forest	Perhumid
11	Tropical Wet Forest	Perhumid
12	Subtropical Wet Forest	Perhumid
13	Subtropical Wet Forest	Perhumid
PANAMÁ		
14	Subtropical Wet Forest	Perhumid
15	Subtropical Wet Forest	Perhumid
16	Subtropical Wet Forest	Perhumid
17	Subtropical Wet Forest	Perhumid
PANAMÁ		
18	Subtropical Wet Forest	Perhumid[b]
19	Subtropical Wet Forest	Perhumid
20	Subtropical Wet Forest	Perhumid
21	Subtropical Wet Forest	Perhumid
22	Subtropical Wet Forest	Perhumid
23	Subtropical Wet Forest	Perhumid
COLOMBIA		
24	Tropical Pluvial Forest	Superhumid
25	Tropical Pluvial Forest	Superhumid
26	Tropical Pluvial Forest	Superhumid
27	Tropical Pluvial Forest	Superhumid
28	Tropical Wet Forest	Perhumid
ECUADOR		
29	Tropical Wet Forest	Perhumid
30	Tropical Wet Forest	Perhumid
31	Tropical Moist Forest	Humid
32	Subtropical Wet Forest	Perhumid
33	Subtropical Wet Forest	Perhumid
34	Subtropical Wet Forest	Perhumid
35	Subtropical Moist Forest	Humid
36	Subtropical Wet Forest	Perhumid

[a] We include Holdridge's "Premontane" (common) and "Lower Montane" (less common) altitudinal belts within the "Subtropical" designation.

[b] The dot on map in figure 50 obscures a small patch of Subtropical Wet Forest.

←

Transitional areas are included within the drier zonal condition (in Panamá and Colombia, the transition between MOIST and WET TROPICAL FOREST is combined with the MOIST TROPICAL FOREST). Uncolored sections are comprised of dry zones, Holdridge's MOIST SUBTROPICAL FOREST, and higher elevations (Holdridge's "montane," "subalpine," "alpine," and "nival" zones; most of these correspond to subpáramo and páramo).

The color segment is compiled and modified from maps by Cañadas (1975), Espinal and Montenegro (1963), Hartshorn et al. (1984), Holdridge (1959a, 1959b, 1962a, 1962b), Holdridge and Budowski (1959), Slud (1964), and Tosi (1969, *in* Holdridge et al., 1971). Maps composed by other researchers were also consulted (Denevan, 1961; Hueck and Seibert, 1981; Knapp, 1965; Lauer, 1959, 1966; Myers, 1969; Stuart, 1966; Troll, 1966). See text for amplified discussion.

tion/humidity, and is quite discriminant. Some have criticized this scheme, however, for diminishing the importance of seasonal climatic change, because it relies on indicator species (thus being unsuitable for analysis of new and unfamiliar regions, but see Hartshorn, 1983a: 119 for a different interpretation) and requires ‘‘special indoctrination or blind reliance on published statements or maps’’ (Myers, 1969: 10).

The systems of Lauer (1959) and Troll (1966) are alike in that both rely on thermal, altitudinal, vegetational, and seasonal (insofar as quantifying the number of humid months per year) criteria. The Köppen scheme follows rigorous temperature and seasonal precipitation criteria, but places little emphasis on humidity and barely addresses information associated with elevation; for example, the symbol *H* refers to ‘‘undifferentiated highlands.’’

For the purpose of understanding the distribution of *O. bolivaris,* the major shortcoming of the Lauer, Troll, and Köppen systems lies with their intrinsic generality because they define ‘‘rain forest’’ in very broad terms. In all three classifications, the distribution of *O. bolivaris* appears within a large conglomerate area described simply as humid tropics.

In contrast, the Holdridge Life Zone System allows further resolution and insight. Holdridge's scheme accommodates rainfall ranges for 2000–4000 mm per year (‘‘moist’’ forest that is ‘‘humid’’), to 4000–8000 mm per year (‘‘wet’’ forest that is ‘‘perhumid’’), and more than 8000 mm per year (‘‘pluvial’’ or ‘‘rain forest’’ that is ‘‘superhumid’’). Because so few places on the planet meet the extreme criteria for a rain forest in Holdridge's classification, some researchers complain that he defined rain forest nearly out of existence (Myers, 1969: 11; see Vareschi, 1980: 139–141, for a contemplative and visual display of differing definitions of rain forest). Gentry (1977: 138), however, conditionally approved of Holdridge's distinctions:

> Several noteworthy distributional and diversity patterns are beginning to be apparent. It now appears that most tropical plant species have geographically ample but ecologically restricted distributions. In most of tropical America, these distributions are much more highly correlated with the Holdridge Life Zone System than with any other system of ecological classification. Only in climatically relatively uniform Amazonia, where edaphic factors become major determinants of distribution, does this phytogeographic system break down. The extent of this ecological specificity has been inadequately appreciated. Even between physiognomically rather similar lowland moist and wet forest, which are lumped together under non-Holdridge classifications, there is surprisingly little [vegetational] species overlap.

Gentry (1977: 144) went on to reiterate the importance of the higher resolution in Holdridge's system: ‘‘Actually the rich Pacific lowland forest is not the single vegetational type which is generally recognized but rather is comprised of two floristically very different vegetational units—moist forest and wet forest.’’

The Holdridge system is not foolproof. One researcher's observations, applications, and interpretations are not guaranteed to agree with those of another. For example, a comparison of the Colombian ecological map prepared by Espinal and Montenegro (1963) and the Ecuadoran counterpart composed by Cañadas (1975) demonstrates an abrupt shift in life zones where the two countries abut (see the map in fig. 41).

Richards (1952: 136), in his classic study of tropical rain forests, stated that ‘‘one of the outstanding features of all moist tropical climates is that seasonal changes of temperature are insignificant compared with seasonal variation in rainfall,’’ a statistic that Holdridge's system does not explicitly address. However, the Köppen designation of *Af* (wet tropical) for the trans-Andean forest region (Haffer 1987b: 5; Trewartha 1961: pull-out map) signifies that there are no dry months.

Based on information gleaned from the various maps, either composed by Holdridge or based on his system, and his ‘‘Diagram for the classification of world life zones or plant formations’’ (Holdridge, 1967), samples of *O. bolivaris* were obtained from habitats in which the mean annual biotemperature is greater than 16°C; the evapotranspiration rating is generally ‘‘perhumid’’ or higher; and the annual precipitation is greater than 2000 mm, sometimes exceeding 8000 mm, but mostly in the range of 4000–6000 mm.

According to Holdridge's terminology, 32 of the 36 collection localities for *O. bolivaris* are in perhumid or superhumid ‘‘Humidity Provinces’’ and in life zones described as Tropical and Subtropical Wet Forest, and Tropical Pluvial Forest (table 23; fig. 50). The distribution of these 32 sites generally coincides with Gentry’s (1978: 135) outline of the extent of wet and pluvial forest in the trans-Andean region:

> . . . wet forest extends the length of the Chocó south along the base of the Andes in Ecuador and northwest along the Caribbean side of Central America to Guatemala [*O. bolivaris* has not been reported north of Honduras] . . . this wet forest is interrupted at intervals along its length: the Canal Zone in Panama and sporadically throughout Nicaragua and Honduras. Isolated patches of wet forest also occur along the Pacific side of Central America, notably in the Azuero Peninsula of Panama and the Osa Peninsula region of Costa Rica. The wet forest tends to be displaced inland onto the lower slopes of the mountains north and south of the Chocó. . . . A final lowland life zone—the pluvial or true rain forest—is restricted to the central Chocó Department [of Colombia] and narrow strips along the Andes and the Central American cordilleras north to extreme southern Nicaragua.

Even though the data are sketchy, some habitat information is associated with specimens and we present it here to provide examples of trapping environments in wet forest localities.

COSTA RICA: In the **Monteverde Cloud Forest Preserve** of Costa Rica (locality 5 in gazetteer), one *O. bolivaris* was caught ‘‘in a trap set on the ground in low, wet area in premontane, evergreen forest’’ (Reid and Langtimm, 1993: 300). This collection site falls in our Subtropical Wet Forest band, which includes Holdridge’s Premontane and Lower Montane altitudinal belts. Hartshorn (1983: 141) noted that ‘‘practically the entire Monteverde Reserve can be considered cloud forest because of the prevalence of moisture-bearing clouds throughout the year.’’

La Selva Biological Station in Costa Rica (locality 7) is in Holdridge’s Tropical Wet Forest life zone. Through years of intense study, the area has become known, among other attributes, as a classic example of Tropical Wet Forest and its associated Central American flora and fauna (Holdridge et al., 1971; Slud, 1960; Hartshorn, 1983; Timm et al., 1989; McDade et al., 1994). Annual rainfall is about 4000 mm (average of 3962 mm, range 2605–5659 mm, over a period of 29 years; Sanford et al., 1994: 23), and mean monthly air temperature (1984–1991) is about 25°C (average of 25.8°C over the period 1984–1991; Sanford et al., 1994: 23). Slud (1960) provided very good photographs of forest views on the Station.

Although several habitats at **Colonia ITCO de Cariari** in Provincia de Limón, Costa Rica (locality 10), were trapped intermittently by Gardner over a period of several months, the only *O. bolivaris* taken were caught beside logs and at the bases of trees in and adjacent to a small banana grove (less than 0.25 ha) in an extremely wet depression in otherwise relatively better drained forest.

PANAMÁ: All collection localities in Panamá are in our bands of Subtropical Wet Forest (table 20; fig. 41), which includes the Premontane and Lower Montane altitudinal belts of Holdridge. In his checklist of Panamanian mammals, Handley (1966: 780) indicated that *O. bolivaris* (he used the name *bombycinus*) is ‘‘rare,’’ was trapped in ‘‘middle elevation evergreen forest,’’ and is ‘‘terrestrial.’’ For example, of 17 specimens collected by Handley from **‘‘Cerro Azul’’** (La Zumbadora, locality 19), 11 were taken from ‘‘mossy rocks beside small stream in forest,’’ 1 came from ‘‘under log in hillside Heliconia thicket,’’ 3 were trapped ‘‘beside log on hillside in primary forest,’’ and 2 were caught ‘‘on log in primary forest beside stream’’ (notations on skin labels). Goldman (1920: 98) had also worked on **‘‘Cerro Azul’’** (Cerro Prominente, locality 19) and noted that a few *O. bolivaris* (reported as *bombycinus*) ‘‘were taken in traps placed mainly under logs and about the bases of large forest trees at from 2,500 to 3,000 feet elevation near the summit of the mountain.’’

Specimens reported by Pearson (1939: 3, as *orinus*) from **Loma Cana** and **Mount Pirre** (localities 21 and 22) were collected in an elevational zone that ‘‘roughly marks the lower edge of the rich, ever-wet, cloud forest’’; the animals ‘‘were all caught along small, steep-sided streams within a few inches of the water’s edge.’’ Collections made years later in the Mount Pirre Range consist of one specimen from 790 m, where it was taken on ‘‘ground, rocky area by stream’’ (notation on skin tag), and two from 1150 m collected in ''trap on ground in elfin forest'' (notations on skin tags).

COLOMBIA: Four (localities 24–27) of five collection localities for *O. bolivaris* in Colombia are from superhumid Tropical Pluvial Forest in the central Chocó region (part of the ''Panama-Chocó regional center'' of Prance, 1989: 102). The ''Chocó phytogeographic region,'' as defined by Gentry (1982: 113), ''may be broadly considered to include that part of the coastal lowlands of western Colombia and northwestern Ecuador covered by wet and moist forest vegetation.'' According to Gentry (1982: 113),

> . . . the outstanding characteristic of the Chocó is its incredibly high average yearly precipitation, reaching 11,770 mm at Tutenendo in central Chocó Department. . . . Central Chocó is the only place in the neotropics where tropical pluvial forest (tropical rain forest as defined by Holdridge, 1967, 1971) occurs. The Chocó is probably the rainiest place in the world.

We have but meager habitat information for specimens obtained north of **Buenaventura** (locality 25) in the Chocó: all were caught in ''mature, tropical wet-pluvial forest'' (notations on skin labels). In the Buenaventura region at Bajo Calima, which is north of Buenaventura, González-M. and Alberico (1993) studied the distribution of small mammals in primary and secondary forests and trapped *O. bolivaris* only in the former. Annual precipitation at Bajo Calima is 7470 mm; other information about the site, including its rich floral diversity, is provided by Gentry (1986).

ECUADOR: Most specimens from Ecuador are from localities in Tropical or Subtropical Wet Forest (table 20; fig. 50). Examples from above **Mindo** (locality 32; UMMZ 155824–155826) were ''caught on ground at streamside in primary forest'' during July 1980 (field notes of R. S. Voss in AMNH, Mammalogy). Closer to Mindo, Voss collected *Sigmodontomys aphrastus*, *Oryzomys hammondi*, and *O. moerex* (Voss, 1988: 423; also see figs. 80 and 81 in that report, depicting stream and forest habitats near Mindo), which are also inhabitants of lower montane rain forest (cloud forest).

MISCELLANEOUS: Only 4 of the 36 collection localities are not contained in the perhumid or superhumid categories, but they are still ''humid'' and in Moist Tropical and Subtropical Forest zones (localities 1, 2, 31, and 35; table 20). Gentry (1978: 135) noted that the wet and pluvial forest zones in the trans-Andean region were

> . . . replaced nearer the coast by an ecologically intermediate but floristically distinct moist forest vegetation similar to the vegetation covering much of the relatively low interiors of Honduras, Nicaragua, Costa Rica (Meseta Central) and Panama. In northwestern Ecuador the Chocó wet forest is similarly replaced by moist forest.

The four collection sites (localities 1, 2, 31, 35) in this coastal zone, which is drier compared to wet and pluvial forests, may represent wetter microhabitats, such as umbral valleys or riparian margins. Locality 1, for example, indicates the **Río Mairin Tingni** in the Río Plátano Biosphere Reserve, our sole Honduran locality, which lies squarely in a humid tropical expanse. Hartshorn (1983b: 427) wrote that the 350,000-hectare Reserve consists of Holdridge's Subtropical Moist, Subtropical Wet, and Subtropical Lower Montane life zones. He also mentioned that the ''major vegetation types include coastal mangroves, swamp forests fringing coastal lagoons, pine savannas, gallery forests and extensive mixed broadleaved forests'' (p. 439). Froelich and Schwerin (1983: 44) reported that the Mairin Tingni site

> was characterized by extremely disturbed, thick undergrowth, a paucity of large trees, and a profusion of intertwined vines. . . . There were also large areas of marsh or otherwise damp soil on the flood plain, suggesting poor drainage. The short, moisture-loving suita palm (*Caluptrogyne sarapiquensis*) abounded everywhere. Even on the mountain slopes, the forest had an extremely disturbed, dense appearance, with large stands of *Bambusa* sp. on the well-drained ridge tops.

The specimens of *O. bolivaris* from Mairin Tingni were captured ''in low wet areas adjacent to streams'' (Benshoof et al., 1984: 512).

Specimens of *O. bolivaris* from the **Río Kurinwas** site (locality 2) in Nicaragua are from low places. Pine (1971: 592) noted that ''the camp was set 'where the ground is higher and high forest, partially cut over for mahogany some 15–20 years previously, is just beginning.' The trapping areas were characterized by various combinations of cleared areas, grassy areas, logging roads, second growth and high forest, and dense brushy areas.'' Three specimens were collected in this area. One *O. bolivaris* was also obtained 5.5 miles downstream from the campsite, where Pine (1971: 592) indicated that the ''terrain . . . 'is extremely low and frequently flooded and is composed almost entirely of dense palm swamp'.''

We lack field data on the **Río Verde** site (locality 31) in Ecuador.

The fourth place, **Pata de Pájaro** (locality 35), in Ecuador, is located in Subtropical/Premontane Moist Forest (although not represented as such on our map in fig. 50, it is still in Holdridge's ''humid'' zone, according to the map prepared by Cañadas, 1975). Three examples of *O. bolivaris* were collected by G.H.H. Tate on June 27, 1923, at the base of the Cerro Pata de Pájaro. Tate and his party had spent a night at Hacienda El Destino and wrote that ''in the morning (pouring rain) we rode into the forest over a trail which had to be opened up to let animals through to a little hut, belonging to a party of rubber-gatherers, at the side of a small stream, which we made our basecamp'' (field journal of G.H.H. Tate, AMNH Mammalogy Archives). Here at 700 feet, Tate ''. . . put out 3 dozen traps. It is abominably wet here and the men say it rains incessantly up above [on higher slopes of the Cerro].'' He collected five rats, three *O. bolivaris*, and two *O. talamancae* (table 26). We have no other information about the forest at the site. In 1991, the Cerro was visited by members of a Rapid Assessment survey, but they worked only in higher wet and cloud/fog forests, not at lower elevations (Foster, 1992).

The geographic range of *Oryzomys bolivaris* is probably more extensive than indicated by our collection records. We would not be surprised to find it in tropical evergreen forest beyond Honduras, possibly all the way to Tabasco and southern Veracruz in the wet tropical forests of southern Mexico. The species should also be sought east of the Chocó region in areas of northern Colombia and western Venezuela that are still covered by wet tropical evergreen rainforest formations (see the vegetation map in Hueck and Seibert, 1981). *Sigmodontomys alfari*, another species apparently restricted to tropical evergreen rain forest, has a range generally concordant with that of *O. bolivaris* and has been recorded from two places in Estado de Zulia, western Venezuela. One is Novito (see appendix H), for which Handley (1976: 78) gave the Holdridge classification as ''PREMONTANE very humid forest'' and described the habitat this way: ''Steep slopes and numerous small streams. Evergreen forest remnant with canopy at 25–30 m and scattered larger trees to 40 m, serving as shade for coffee and bananas.'' Holdridge's classification for Novito would include it in our outline of Subtropical Wet Forest on the map in figure 50, a zone that elsewhere encompasses several collection localities for *O. bolivaris*. The other site is Misión Tukuko (09°50′N/72°52′W), a site near Novito that was described by Voss (1991: 68–70), who, on July 14, 1986, trapped a juvenile (MHNLS 7708) ''on ground along upper edge of *Heliconia* swamp, in runway beside rock ledge under grass in pasture'' (field journal of R. S. Voss in AMNH, Mammalogy). Voss (1991: 70) noted the ''entire region surrounding the mission was covered by evergreen rain forest as lately as 40 or 50 years ago, but most level ground has since been cleared for cultivation or animal husbandry.''

As defined by localities where specimens were collected, the range of *O. bolivaris* is confined to wet and humid tropical evergreen rainforest formations in the trans-Andean region, a distribution mirrored by some species of invertebrates (Brown, 1987), frogs (Lynch, 1979; Duellman, 1982), reptiles (Dixon, 1979; see maps showing restricted distributions of rainforest lizards and snakes, pp. 232–233), birds (see table 8.1 in Haffer, 1974; Haffer, 1985, 1987, especially the range of the forest hawk, *Leucopternis semiplumbea*), as well as other mammals. Examples of the last include the ranges of another oryzomyine, *Sigmodontomys alfari*, and an echimyid, *Hoplomys gymnurus* (fig. 51). Most collection localities of those two rodents fall within the modified Holdridge life zones we depict in figure 50 and reflect distributions generally concordant with that documented for *O. bolivaris*. All three species were collected at some sites (table 24; Benshoof et al., 1984; González-M. and Alberico, 1993). Another echimyid, *Proechi-*

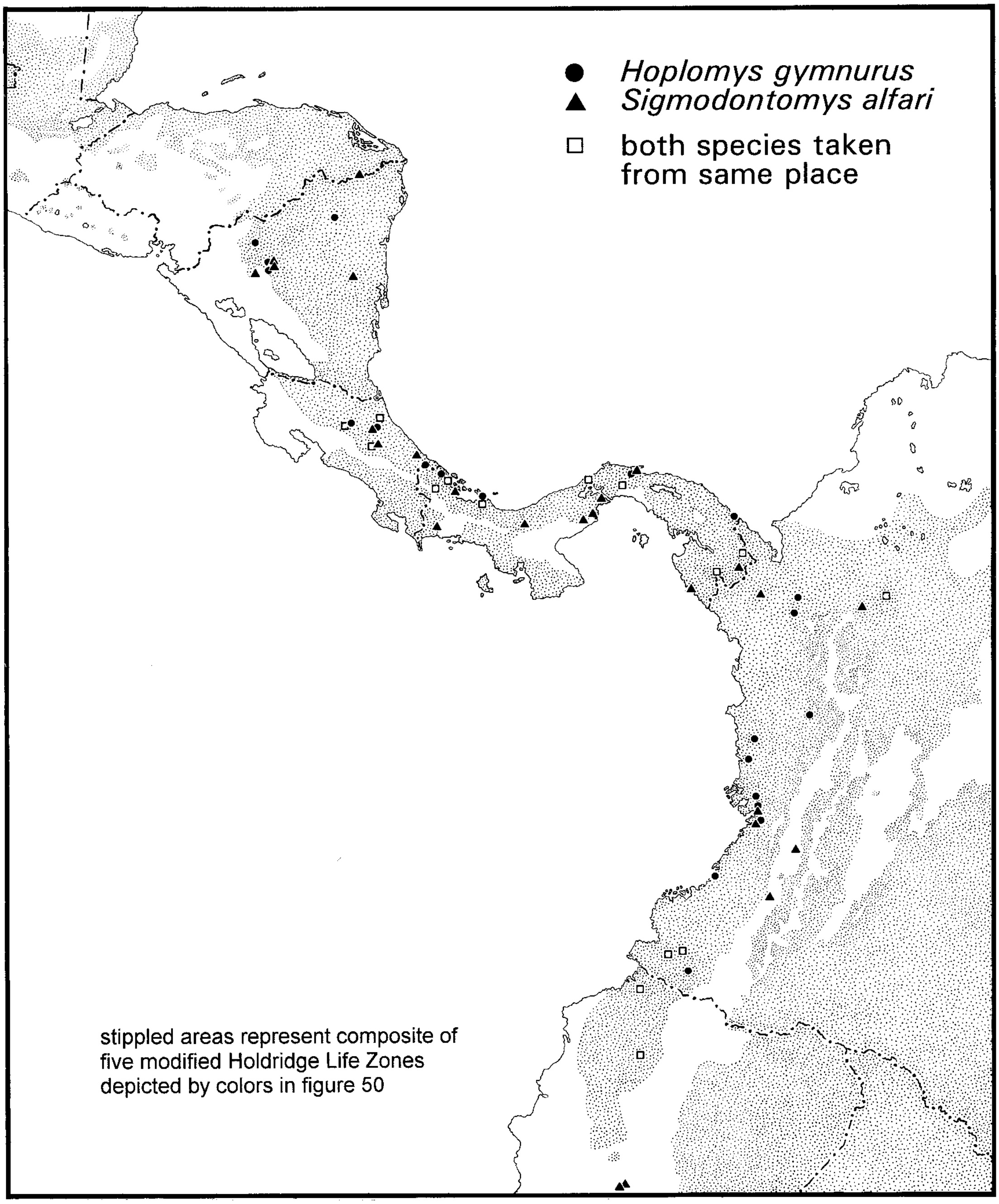

Fig. 51. Distributions of the echimyid *Hoplomys gymnurus* and the oryzomyine *Sigmodontomys alfari*, based on collection localities for specimens we examined and that we list in appendix H. We did not map insular sites for *Hoplomys* collected on the San Blas Archipelago of Panamá and Isla Escudo de Veraguas. We also omitted localities on Isla San Cristóbal in Panamá as well as Novito in Estado de Zulia, Venezuela, where some examples of *Sigmodontomys* were obtained. Both species were reported with *Oryzomys bolivaris* in the Río Plátano Biosphere Reserve at 15°38'N/84°55'W (Benshoof et al., 1984; see locality 1 in gazetteer for *O. bolivaris*), which is farther west in Honduras than indicated on the map, but we have not examined those specimens.

TABLE 24
Localities Where Specimens of *Oryzomys bolivaris* Were Collected with Examples of *Hoplomys gymnurus* and/or *Sigmodontomys alfari*
(Number in parentheses at left refers to localities in gazetteer for *O. bolivaris*, where specimens are listed by museum initials and catalog numbers. Specimens of *Hoplomys* and *Sigmodontomys* are listed in the gazetteers in appendix H. Date indicates segment of time during which samples of the species were collected.)

Locality	*H. gymnurus*	*S. alfari*	Date
NICARAGUA			
(2) Río Kurinwas	–	+	Sept 1967
COSTA RICA			
(6) Villa Quesada	+	+	Apr 1983
(8) Parque Nacional Braulío Carrillo	+	–	Mar 1986
(10) Cariari	+	+	1966, 1967
PANAMÁ			
(14) Río Changena	+	+	Sept 1961
(17) 6 mi E El Valle	–	+	Mar 1957
(19) "Cerro Azul" (La Zumbadora)	+	+	1957, 1958
COLOMBIA			
(25) N Buenaventura	+	–	Dec 1981
(26) Río Raposo	–	+	May–July 1962
(28) Barbacoas	+	+	Aug, Sept 1912
ECUADOR			
(30) San Javier	+	+	May, July, Aug 1900

mys semispinosus, has a very similar distribution in tropical rainforest habitats in the trans-Andean region. Gardner (1983b: 142) summarized its range: "The Central American distribution . . . extends from southeastern Honduras and eastern Nicaragua through Costa Rica and Panama including the Islas Las Perlas [see map in Hall, 1981: 873]. In South America, the range is west of the Andes from the Choco of Colombia (including Isla Gorgona) to southwestern Ecuador." Benshoof et al. (1984) documented the most northern occurrence of *P. semispinosus* in Honduras, and Patton (1987: 311, 343–344) provided a map of the species distribution as well as collection localities. *Sigmodontomys aphrastus* has been recorded from a few sites in cool and perennially wet forests from Ecuador (Voss, 1988: 423) to the Talamanca highlands of Costa Rica (Carleton and Musser, 1995). Survey of the taxonomic literature may reveal additional species of vertebrates and invertebrates with similar distributions in wet and humid tropical rain forest, as may future revisionary studies of mammals (*Melanomys caliginosus* and *Oryzomys alfaroi,* for example). The significant point is that the concordance of these ranges is not an artifact of collecting but reflects the historical interplay of organismal and topographic evolution. The ranges of *Oryzomys bolivaris, Sigmodontomys alfari, Hoplomys gymnurus,* and *Proechimys semispinosus* are mammalian examples of the reality behind Haffer's (1974) delineation of the trans-Andean region as a subdivision of the larger Neotropical realm.

DESCRIPTION OF THE SPECIES

Oryzomys bolivaris stands out from other species of *Oryzomys* by its luxuriant soft fur and exceptionally long facial vibrissae. It is of medium body size with a tail about as long as the combined lengths of head and body (table 25). The upperparts of adults are a rich dark brown, darker along the head and back, and paler, yellowish brown along sides of the head and body. Overhairs are dark gray for three-fourths of their length and are tipped with tawny brown. Sides of the head and each eye ring are also dark brown; the cheeks are grayish white, buffy, or tawny. Pinnae are dark brown or blackish, with both outer and inner surfaces being sparsely covered with short brown hairs.

Texture of the dorsal fur is distinctive. The

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The range of each species, as indicated by most collection sites, is confined to very wet and permanently humid forest in the trans-Andean region. These distributions are generally concordant with that of *O. bolivaris* (see fig. 50), which has been collected with *Hoplomys* and *Sigmodontomys* at some of the same localities (table 24).

TABLE 25

Descriptive Statistics for Measurements (mm) of *Oryzomys bolivaris* from Central America and Northwestern South America

(Mean, ± 1 SD, observed range in parentheses, and number of specimens are listed for each measurement. Samples contain both sexes and an age range from young to old adults. Specimens measured are identified in the footnotes).

	Nicaragua[a] (localities 2, 3)	Costa Rica and Western Panamá[b] (localities 6, 10, 12, 14, 15)	Central Panamá[c] (locality 19)	Eastern Panamá[d] (localities 1-23)	Colombia[e] (localities 24-26)	Ecuador[f] (localities 29-32, 34-36)
LHB	108.2 ± 8.58 (99–119) 5	118.7 ± 8.23 (103–134) 12	120.7 ± 8.00 (111–140) 13	116.8 ± 7.73 (107–125) 5	127.4 ± 8.85 (115–141) 8	119.4 ± 7.0 (111–133) 9
LT	115.2 ± 9.88 (99–126) 5	113.2 ± 8.77 (96–125) 9	120.8 ± 6.34 (111–130) 13	117.6 ± 7.83 (109–126) 5	121.3 ± 9.94 (100–135) 8	114.8 ± 8.53 (100–127) 8
LHF	28.8 ± 1.92 (27–32) 5	30.3 ± 1.55 (27–33) 13	30.0 ± 1.69 (27–33) 15	28.0 ± 1.23 (25–29) 5	30.5 ± 1.20 (29–32) 8	29.7 ± 1.66 (28–32) 9
LDF	10.0 ± 0.71 (9–11) 5	10.2 ± 1.28 (8–13) 13	10.3 ± 1.03 (7–11) 15	12.0 ± 0.71 (11–13) 5	9.1 ± 0.99 (8–10) 8	8.1 ± 1.52 (6–10) 10
LMV	40.2 ± 5.54 (35–48) 5	42.1 ± 3.77 (35–48) 13	47.6 ± 3.54 (40–54) 15	45.5 ± 3.11 (43–50) 4	50.9 ± 7.02 (40–60) 8	43.1 ± 4.61 (35–50) 10
LSV	45.2 ± 5.93 (40–55) 5	46.6 ± 5.30 (40–55) 13	54.3 ± 6.55 (38–65) 15	54.8 ± 9.52 (45–64) 5	56.7 ± 11.59 (44–75) 7	46.5 ± 7.43 (40–60) 8
LGV	28.4 ± 3.21 (24–33) 5	27.4 ± 3.21 (25–35) 9	36.3 ± 4.42 (28–43) 15	43.3 ± 5.44 (36–49) 4	41.5 ± 4.81 (35–50) 8	33.9 ± 5.04 (27–42) 10
ONL	30.5 ± 1.85 (28.6–33.3) 5	30.5 ± 1.38 (28.1–33.0) 12	30.4 ± 1.23 (28.1–32.5) 15	30.5 ± 0.46 (30.0–30.9) 3	32.3 ± 0.94 (31.3–34.0) 6	31.0 ± 1.07 (29.5–33.4) 10
ZB	14.8 ± 0.82 (14.1–15.7) 4	14.8 ± 0.37 (14.2–15.6) 12	14.7 ± 0.81 (13.4–15.9) 15	15.1 ± 0.33 (14.7–15.4) 4	15.4 ± 0.59 (14.4–15.9) 5	14.9 ± 0.76 (14.1–16.3) 10
IB	5.4 ± 0.41 (5.1–6.1) 5	5.3 ± 0.21 (5.0–5.7) 12	5.1 ± 0.16 (4.9–5.5) 15	5.1 ± 0.13 (4.9–5.2) 4	5.4 ± 0.19 (5.1–5.6) 7	5.3 ± 0.17 (5.0–5.5) 12
LR	9.3 ± 0.76 (8.5–10.3) 5	9.3 ± 0.49 (8.4–10.3) 14	9.5 ± 0.47 (8.3–10.1) 15	9.5 ± 0.21 (9.2–9.7) 5	9.8 ± 0.33 (9.4–10.4) 7	9.3 ± 0.71 (8.2–11.0) 12
BR	5.3 ± 0.45 (4.9–6.0) 5	5.4 ± 0.26 (4.8–5.7) 14	5.3 ± 0.22 (4.8–5.6) 15	5.2 ± 0.33 (4.9–5.6) 5	5.8 ± 0.30 (5.4–6.2) 7	5.5 ± 0.30 (5.1–6.2) 12
LB	12.0 ± 0.40 (11.4–12.5) 5	12.0 ± 0.27 (11.5–12.5) 12	11.7 ± 0.34 (11.0–12.1) 15	11.6 ± 0.26 (11.3–11.9) 4	12.2 ± 0.50 (11.4–12.7) 6	11.8 ± 0.31 (11.4–12.3) 10
HBC	8.5 ± 0.38 (8.1–9.0) 5	8.6 ± 0.24 (8.0–8.8) 12	8.5 ± 0.27 (8.0–8.9) 15	8.8 ± 0.30 (8.5–9.1) 3	8.6 ± 0.15 (8.4–8.8) 6	8.5 ± 0.21 (8.3–8.9) 9
BZP	3.3 ± 0.37 (3.0–3.9) 5	3.2 ± 0.24 (2.7–3.6) 14	2.9 ± 0.23 (2.5–3.3) 15	3.0 ± 0.11 (2.9–3.2) 5	3.2 ± 0.17 (2.9–3.4) 7	3.1 ± 0.25 (2.7–3.6) 12
ID	7.6 ± 0.50 (7.1–8.2) 5	7.5 ± 0.38 (6.8–8.0) 14	7.7 ± 0.41 (6.9–8.4) 15	7.9 ± 0.30 (7.5–8.2) 5	8.3 ± 0.38 (7.8–8.8) 7	7.7 ± 0.42 (7.2–8.5) 12
LBP	6.2 ± 0.38 (5.8–6.7) 5	6.0 ± 0.34 (5.4–6.5) 14	6.0 ± 0.40 (5.3–6.9) 15	6.1 ± 0.29 (5.8–6.4) 4	6.4 ± 0.32 (5.8–6.7) 7	6.1 ± 0.41 (5.4–6.8) 12
BBP	5.4 ± 0.29 (5.0–5.8) 5	5.6 ± 0.20 (5.3–5.9) 14	5.6 ± 0.26 (5.2–6.1) 15	5.6 ± 0.23 (5.2–5.8) 5	5.9 ± 0.10 (5.7–6.0) 6	5.6 ± 0.30 (5.2–6.1) 10
PPL	10.2 ± 0.78 (9.4–11.1) 5	10.3 ± 0.64 (9.2–11.3) 12	10.1 ± 0.64 (9.3–11.3) 15	10.1 ± 0.58 (9.8–10.8) 3	11.0 ± 0.24 (10.7–11.4) 6	10.6 ± 0.51 (9.5–11.3) 9

TABLE 25
(*Continued*)

	Nicaragua[a] (localities 2, 3)	Costa Rica and Western Panamá[b] (localities 6, 10, 12, 14, 15)	Central Panamá[c] (locality 19)	Eastern Panamá[d] (localities 1–23)	Colombia[e] (localities 24–26)	Ecuador[f] (localities 29–32, 34–36)
LIF	4.2 ± 0.08 (4.1–4.3) 5	4.4 ± 0.15 (4.1–4.6) 14	4.7 ± 0.33 (4.2–5.6) 15	4.4 ± 0.30 (4.1–4.9) 5	4.6 ± 0.32 (4.1–5.1) 7	4.6 ± 0.42 (3.9–5.1) 12
BIF	2.3 ± 0.16 (2.1–2.5) 5	2.3 ± 0.13 (2.0–2.6) 14	2.3 ± 0.16 (2.1–2.6) 15	2.3 ± 0.05 (2.2–2.3) 5	2.5 ± 0.19 (2.1–2.7) 6	2.3 ± 0.17 (1.9–2.5) 12
CLM1–3	4.3 ± 0.11 (4.2–4.5) 5	4.3 ± 0.10 (4.2–4.5) 14	4.4 ± 0.11 (4.2–4.6) 14	4.2 ± 0.05 (4.2–4.3) 5	4.3 ± 0.12 (4.2–4.5) 6	4.3 ± 0.19 (4.1–4.6) 9
BM1	1.3 ± 0.07 (1.2–1.4) 5	1.3 ± 0.05 (1.2–1.3) 14	1.3 ± 0.05 (1.3–1.4) 15	1.2 ± 0.06 (1.2–1.3) 5	1.3 ± 0.09 (1.2–1.4) 7	1.3 ± 0.06 (1.2–1.4) 10

[a] Río Kurinwas: USNM 392860–392863. Bluefields: MVZ 140659.

[b] Villa Quesada: LSUMZ 26352, 26356. Cariari: LSUMZ 13171–13175, 15326. Tuis: AMNH 9631/7971 (holotype of *O. nitidus alleni*). Río Changena: USNM 319475–319478. Bugaba: BMNH 0.7.11.47.

[c] "Cerro Azul": USNM 171103, 171104, 171105 (holotype of *O. bombycinus*), 305649, 305651, 305658, 306916–306925.

[d] Loma Cana: ANSP 19706, 19707. Mount Pirre: ANSP 19708, 19709 (holotype of *O. bombycinus orinus*). Cerro Tacarcuna: USNM 338260.

[e] Condoto: BMNH 13.8.10.6, 13.8.10.7, 14.5.28.13, 14.5.28.14. Buenaventura: USNM 554232, 554235, 554236. Río Raposo: USNM 334698.

[f] Carondelet: USNM 113293, 113294. San Javier: BMNH 1.3.19.11 (holotype of *O. castaneus*); USNM 113292, 113296, 113297. Río Verde: BMNH 1.1.6.6 (holotype of *O. rivularis*). Mindo: UMMZ 155824. Santo Domingo: BMNH 15.1.1.41, 15.1.1.42. Pata de Pájaro: AMNH 66235. Hacienda Porvenir: BMNH 99.9.9.27 (holotype of *O. bolivaris*).

coat is thick, up to 13 mm long in adults (tables 25, 27), its surface even and formed primarily by tips of the overhairs; guard hairs are thin and inconspicuous, extending only slightly beyond the pelage contour. The long fur is very dense and soft to the touch, not at all woolly.

Underparts are chromatically and texturally sharply demarcated from upperparts. Hairs are dark gray for most of their lengths and have unpigmented tips, a combination that is perceived as grayish white over the ventral coat. The ventral pelage is also thick (up to 4 mm long) and soft.

Mystacial, superciliary (often referred to as orbital or supraorbital), and genal vibrissae are all extraordinarily long (tables 25, 27; fig. 53); each is glistening black for most of its length and translucent at the tip. The longest of the superciliary vibrissae (up to three may be present) extends far beyond the pinnae when laid back against the head, whether on stuffed skins or intact animals preserved in fluid. One of the genal vibrissae (either one or two in a set), although shorter than the longest superciliary, also extends beyond the ear when laid against the head.

The tail is finely scaled (table 27) and seems nearly naked because the three hairs that emerge from beneath each scale are so short. Dorsal and lateral surfaces along the full length of the tail are brown or dark brown. The ventral surface in most specimens is pale brown, either uniformly along the tail (rare) or mottled. The most common pattern seen among samples is one where the proximate half of the tail ranges from mottled to unpigmented and the distal half is pale brown. Other variations occur: the tail may seem bicolored because the ventral surface is mostly unpigmented except for a few pale brown blotches, the ventral surface is mottled for its entire length, or the surface is pale brown throughout broken by darker spots. A monocolored tail occurs infrequently in our samples and is usually associated with specimens having partially melanistic coats (samples from Colombia, for example).

Hind feet are long and narrow; the three middle digits are much longer than the outer two. The plantar surface is naked from heel to tips of the digits and adorned with six low plantar pads (fig. 54). Each dark brown plantar surface is smooth in most specimens, but some individuals have indistinct scalation on the distal portion of the foot between the digits. The pattern is a faint impression, nothing so pronounced as that seen in examples of *Sigmodontomys* and *Melanomys*. Dorsal and lateral surfaces of the metatarsal region and digits are unpigmented and thinly covered with short white hairs so each foot seems to be nearly naked. Claws are short and unpigmented; at the base of each is a tuft of silver hairs covering the claw but not extending appreciably beyond it.

Front feet have unpigmented palmar surfaces and claws. Dorsal metacarpal and digital surfaces are also unpigmented and sparsely covered with short silvery hairs, and each claw is also covered by unpigmented hairs. The wrist and dorsal surface of each forearm are dark gray, which contrasts with general tone of the upperparts.

Females have eight teats, the usual number observed in most oryzomyine rodents (see Carleton and Musser, 1989; Voss and Carleton, 1993; an exception is *Scolomys* with three pair of teats [Patton and da Silva, 1995]). One pair of teats is pectoral in position, another pair is postaxillary, one pair is abdominal, and the other is inguinal.

Most variation in coat color is associated with age. Specimens we determined to be young adult and those in which the molt from juvenile to adult coat has just occurred tend to be darker than adults and older animals, which have brighter pelage. In these younger rats, the overhairs are dark gray for most of their length and tipped with a bit of dull brown. Underparts are also slightly darker because the white distal portion of each hair is shorter than the comparable segment in adult pelage. The difference recalls the chromatic contrast between adult and subadult coats of species of *Peromyscus,* but we have not detected a change from the dark pelage of young adult *O. bolivaris* to the brighter coat of adults through molt.

The dorsal juvenile coat is much darker than the adult pelage, being a burnished dark brown to blackish, nearly black on the face and along the head and back, much as Goldman (1918: 77) described it. The overhairs are dark gray for most of their length and tipped with dull buff. Fur texture also contrasts with that of adults, being finer and softer.

Some samples of adults are polymorphic in coat color. For example, of the three specimens obtained from near Buenaventura (locality 21), Colombia, two (USNM 554232 and 554236) are covered by lustrous dark brown pelage. The third individual (USNM 554235) is partially melanistic; the dark upperparts do not result from the buffy tips of the overhairs wearing down to the dark bands. The tail is blackish all over, the hind feet are blackish brown, tops of the front feet are dark, as is part of the left palmar surface, the ears are blackish, and the head and back are chocolate brown; sides from cheek to thighs are dark tawny. Underparts are grayish buff rather than grayish white. The dorsal coat is very soft and slick to the touch, a texture common to melanistic fur.

The skull of adult *O. bolivaris* (differently aged individuals are illustrated in figs. 57, 59, and 61) is moderately elongate and angular. The rostrum is long and narrow. Zygomatic arches are nearly parallel, from dorsal aspect, with only slight anterior convergence to moderately broad zygomatic plates that barely overlap the posterior portion of each nasolacrimal capsule. The region between the orbits is wide, the braincase narrow and boxlike, and its lateral and rear walls are nearly vertical. Prominent supraorbital shelves accentuate dorsolateral margins of the interorbit and transform posteriorly into low temporal ridges or beaded edges along the frontals and lateral margins of the parietals to the lambdoidal ridges. The side of the braincase between temporal ridge and ventral root of the zygoma is formed entirely from the squamosal. Incisive foramina are long, but their posterior margins lie in front of the molar rows. The bony palate extends beyond the molar rows where it is sculptured by pits and foramina. Roof of the moderately wide mesopterygoid fossa is breached by short, narrow, and inconspicuous sphenopalatine vacuities. Auditory bullae are small but the capsules cover a significant portion of the periotics. Large stapedial foramina, a conspicuous posterolateral groove on each pterygoid plate, squamosoalisphenoid grooves on the inside walls of the braincase, and sphenofrontal foramina testify to the primitive arrangement of the cephalic arterial pattern, a configuration similar to that diagramed for *O. talamancae* (Musser and Williams, 1985) and species of *Microryzomys* (Carleton and Musser, 1989).

Chunky in appearance, each dentary of *O. bolivaris* has a delicate coronoid projection, long condyloid process, and deep ascending ramus (fig. 61). The capsular process that encloses the root of the incisor is evident below the coronoid process but does not protrude noticeably from the lateral surface of the dentary.

Incisors are moderately large with smooth enamel faces. In lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration (fig. 61; also, see the diagram in Hershkovitz, 1990: 34). Orange enamel is characteristic of both upper and lower incisors, but the lowers are paler.

Molars have low crowns (brachydont), with each upper tooth anchored by three roots and each lower by two. Two rows of cusps, set in opposite labial–lingual pairs, and separated by deep flexi in places, but also connected by diagonal mures and horizontal ridges, form the basic foundation of the coronal topography of each molar (figs. 63, 64). Diagnostic structural details of the occlusal surface are described below in the section on species comparisons.

Gardner and Patton (1976) reported the chromosomal composition of *O. bolivaris* (under the name *bombycinus*) based on five individuals captured in Costa Rica (table 13). With a diploid number of 58, a fundamental number of 80, and ‘‘high number of large biarmed autosomes,’’ those authors considered *O. bolivaris* to be ‘‘one of the most strongly differentiated members of the subgenus *Oryzomys*’’ (p. 17), commented that its relationship to other species for which chromosomal data were then available was obscure, and suggested its affinities might be with *O. melanotis* and *O. alfaroi* and its relatives, a postulation made earlier by Hershkovitz (1966). At the time, no karyotypic data had been published for those two species, but information is now available (Haiduk et al., 1979; also see fig. 71). The chromosomal complement of *O. melanotis* ($2n = 62$, FN = 70) consists primarily of telocentric pairs, whereas that of *O. alfaroi* ($2n = 60$, FN = 104, México; $2n = 62$, FN = 100, Ecuador) is formed mainly by biarmed pairs (see chromosomal comparisons between the latter and *O. bolivaris* in the next section). These characteristics contrast with the karyotype of *O. bolivaris*, but provide no information about degree of phylogenetic affinity among the species.

COMPARISONS WITH OTHER SPECIES OF *ORYZOMYS*

Oryzomys bolivaris is partly defined by its contrasts with similar species of *Oryzomys* that occur in the same region. Here we contrast characteristics of *O. bolivaris* with those of *O. talamancae* and *O. alfaroi*. Morphology of *O. bolivaris* is similar to that of *O. talamancae*. Examples of both species have been taken at the same localities in Panamá and Ecuador (table 26), and they likely occur together elsewhere. Specimens of each are regularly confused, even by naturalists familiar with both kinds. Musser and Williams (1985), for example, misidentified examples of *O. bolivaris* as *O. talamancae* (see gazetteer), and Handley’s (1966) material from Panamá, which he determined to be *O. capito* (his designation for *talamancae*), contained a few specimens of *O. bolivaris*.

Our definition of *O. talamancae* reflects the view of Musser and Williams (1985), as elaborated and modified below and in our account of *O. talamancae* that follows the *bolivaris* section.

Examples of *O. bolivaris* and *O. alfaroi* have been collected at the same localities in Costa Rica and Ecuador (table 22) and undoubtedly occur together in other regions. Adults of each species are easily separated from one another, but young *O. bolivaris* are commonly misidentified as young or adult *O. alfaroi* in collections of museums, particularly where samples of each kind were obtained from the same locality.

Oryzomys alfaroi has not been taxonomically revised since Goldman’s work (1918). Carleton and Musser (unpubl.) are preparing a taxonomic revision of *O. alfaroi*. For our purposes, Goldman (1918: 60) described the basic cranial and dental traits (these are also shown in figs. 63, 64, 72, and 73) that characterize *O. alfaroi* (see Goldman's description of *O. a. alfaroi*). The known geographic range of *O. alfaroi* was summarized by Musser and Carleton (1993: 720) as occurring in lowland to lower montane forests from southern Tamaulipas and Oaxaca, México, through Central America, to western Colombia and Ecuador. Those authors also listed the eight scientific names that are synonyms of *O. alfaroi*.[5]

Oryzomys bolivaris and *Oryzomys talamancae*

Samples used for comparisons are from ''Cerro Azul'' because they contain the largest available number of *O. bolivaris* and *O. talamancae* collected from any of the places where they have been taken together (all but three of the *O. bolivaris* and the entire sample of *O. talamancae* were collected by C. O. Handley, Jr. from La Zumbadora; three of the *O. bolivaris*, including the holotype of *O. bombycinus*, were obtained by E. A. Goldman from the nearby Cerro Prominente; both places are included within ''Cerro Azul''; see explanation under locality 19 in gazetteer for *O. bolivaris*). Sufficient examples of each species are available to allow us to assign specimens to four age categories:

1. *Adult*: Full adult pelage; conformation of cranium as illustrated in figures 57–61; molar occlusal surfaces of most specimens obviously worn, primary cusps still evident but rounded, lophs and mures indistinct, enamel island formed by mesoflexus of second upper molar isolated or obliterated; the occlusal pattern is hardly discernable in a few specimens, the primary cusps obliterated and crowns flat or concave (old adults).
2. *Young adult*: Pelage usually darker than that of older animals; cranium smaller (figs. 57–60; table 27); molar occlusal surfaces slightly worn, primary cusps still conical, lophs distinct, wear stage of second and third molars similar to that described by Myers and Carleton (1981: 4, age class II).
3. *Young adult-juvenile*: Intermediate in body size between young adults and juveniles (figs. 57–60; table 28); all examples in some stage of molt between the juvenile coat and fresh adult pelage; molar occlusal surfaces hardly worn; some individuals in mostly adult pelage are reproductively mature (indicated by the notation ''embryos'' on skin labels).
4. *Juvenile*: Small body size (figs. 57–60; table 28); entirely covered with juvenile pelage, which is darker and shorter than the adult coat, finer and much softer to the touch; third molars unworn, either unerupted or at some stage of eruption, from just above the gumline to slightly below occlusal surfaces of second and first molars.

We focus first on comparisons between adults of each species from ''Cerro Azul,'' then mention whether these distinctions are also found between samples of each species in the three other age classes. Unfortunately, sample sizes are uneven and those in younger age classes are especially small. Nevertheless, the differences in vibrissal length, pelage thickness and texture, and characteristics associated with the hind feet are spectacular and distinguish examples of the two species

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[5] Five of the eight scientific names associated with *Oryzomys alfaroi* by Musser and Carleton (1993: 720) are tied to holotypes collected within the geographic ranges of both *O. bolivaris* and *O. talamancae*. These are *O. gracilis* Thomas (1894: 358; Colombia, Antioquia, Concordia, Medellín, 1740 m; BMNH 73.11.5.4), *O. alfaroi incertus* Allen (1908: 655; Nicaragua, Río Grande; AMNH 28584), *Oryzomys palmirae* Allen (1912: 83; Colombia, Valle de Cauca, Mira Flores, a few miles east of Palmira, 1260 m; AMNH 32224), *O. a. dariensis* Goldman (1915: 128; Panamá, Cana, 610 m; USNM 178660), and *O. a. intagensis* Hershkovitz (1940: 78; Ecuador, Imbabura Province, Intag, Hacienda Chinipamba near Peñaherrera, 1500 m; UMMZ 77152). We have examined these holotypes and verified their identity as *O. alfaroi*. The first four names had already been formally and correctly linked to *O. alfaroi* by Goldman (1918) in his revisionary treatise of North American *Oryzomys*. Carleton and Musser (unpubl. MS) provided extended documentation supporting Goldman's arrangement as well as allocation of *intagensis* and three other scientific names to *O. alfaroi*. Clarifying the identities of these holotypes is important in the context of diagnosing *O. bolivaris* and *O. talamancae* because specimens of those two have been, and probably will continue to be, misidentified as *O. alfaroi* by collectors and museum curators.

TABLE 26

Records of *O. talamancae* and *O. alfaroi* Captured with *O. bolivaris* at Localities in Costa Rica, Panamá, and Ecuador

(Number in parentheses at left refers to localities in gazetteer for *O. bolivaris* and symbol on map in fig. 50. Specimens of *O. bolivaris* from each place are listed in the gazetteer. Date indicates segment of time during which samples of both species were collected.)

Locality	*O. talamancae*	*O. alfaroi*	Date
COSTA RICA			
(6) NE Villa Quesada	—	LSUMZ 26353–26355	April 1983
(12) Tuis	—	AMNH 9613/7953–9621/7961, 9625/7965, 9627/7967–9630/7970	July 1894
PANAMÁ			
(16) El Valle	USNM 303430, 304804	—	Mar 1957
(17) El Valle, 6 mi E	USNM 304803, 304805–304808, 304811, 304812	—	Mar 1957
(18) Cerro Bruja	USNM 171530	—	June 1911
(19) "Cerro Azul" (La Zumbadora)	USNM 302493, 302496, 302674–302677, 303102–303104, 303260, 303261, 302497–302506, 302667, 305703, 306952–306955, 306957, 306959, 310568, 310569, 310571–310574	—	Dec 1955; Jan–Apr, June 1956; June 1957; Jan–Feb, July, Sept, Oct 1958
ECUADOR			
(33) Río Tulipe	—	FMNH 94969, 94971–94975	Aug 1961
(35) Pata de Pájaro	AMNH 66236, 66237	—	June 1923

in all four age categories. Outside of "Cerro Azul," these same vibrissal and pelage differences distinguish all samples of the two species we have studied, regardless of geographic provenance. The mensural contrasts in external and cranial dimensions discussed below should be tested by larger samples not only from Panamá but from elsewhere throughout the geographic distribution of *O. bolivaris* where it is found with *O. talamancae*.

Size of body and appendages: Body size of adults (inferred from length of head and body) is comparable in the two species, but *O. bolivaris* has a shorter tail and longer hind foot, not only in absolute mean values (table 27) but also relative to length of head and body (fig. 52). Young adults of *O. bolivaris* and *O. talamancae* also differ significantly in mean length of hind foot, but not in mean tail length (table 27); samples of each species in younger age groups cannot be distinguished by these measurements (table 28).

Vibrissae: A conspicuous qualitative distinction between samples of each species in all of the three oldest age categories is length of vibrissae. Examples of *O. bolivaris* have significantly longer mystacial, superciliary, and genal vibrissae than do those of *O. talamancae* (tables 27, 28; fig. 53). The difference is immediately obvious by simple inspection. Vibrissal lengths may not differ between juveniles. Our single juvenile skin of *O. bolivaris* from "Cerro Azul" has slightly longer mystacial and superciliary vibrissae than do the four juvenile *O. talamancae*, but the distinction is not strikingly apparent and may be insignificant in larger samples.

Fur: Adult and young adult *O. bolivaris*, as well as those in the molt transition from juvenile to adult pelage, have a noticeably longer dorsal coat than do examples of *O.*

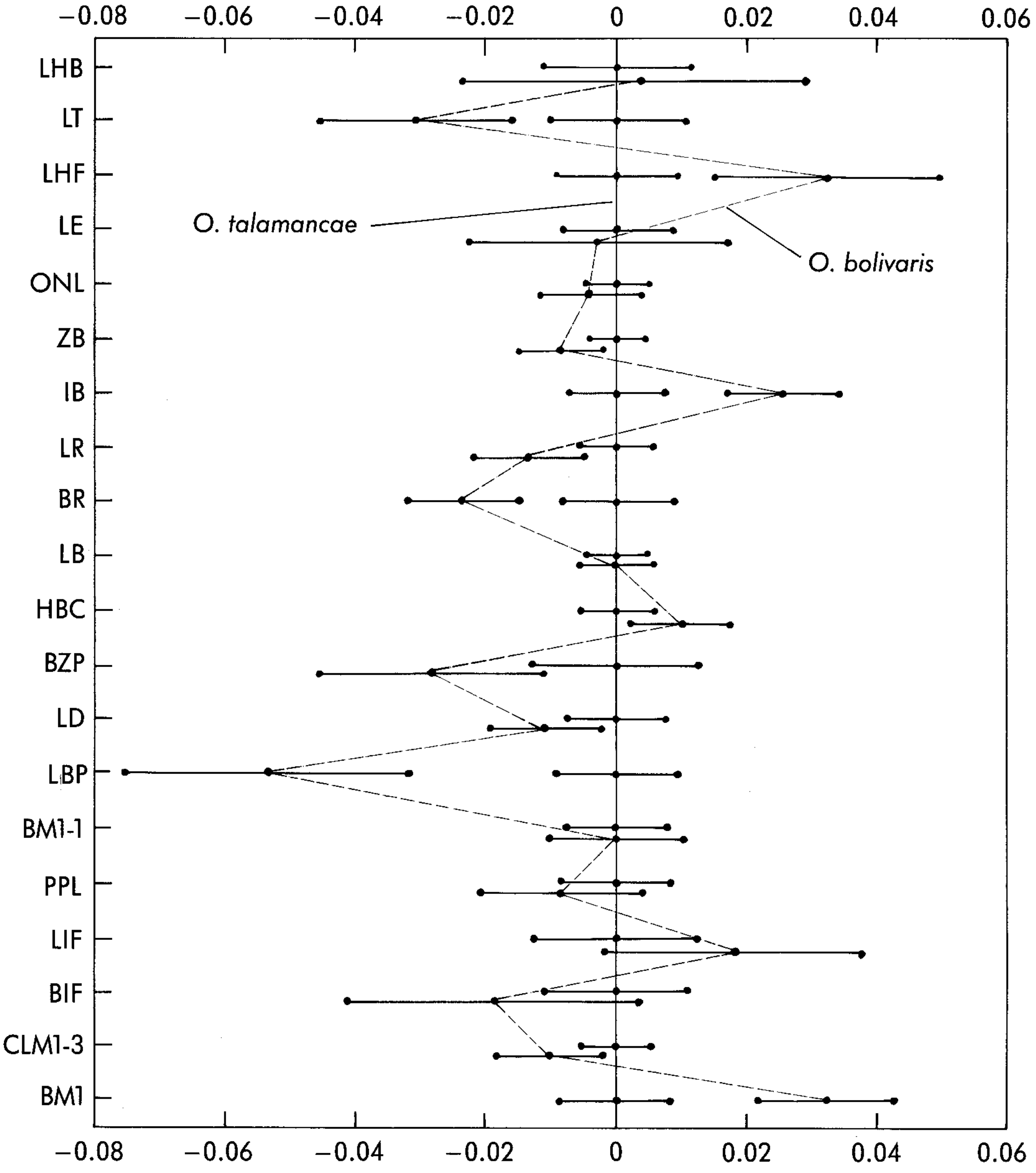

Fig. 52. Ratio diagram illustrating certain proportional relationships between samples of adult *Oryzomys talamancae* (the standard) and *O. bolivaris* from "Cerro Azul," Panamá. Data are derived from values for mean, standard deviation, and sample size of variables listed in table 27. See Materials and Methods for an explanation of the construction of ratio diagrams.

talamancae of comparable age, a contrast that is easily quantified (tables 27, 28). The difference is also apparent to the touch: the fur of *O. bolivaris* feels very soft and thick, whereas that of *O. talamancae* has a shorter, less dense texture.

Oryzomys bolivaris has a darker coat than does *O. talamancae*: dark brown over top of head and body and pale yellowish brown sides. These somber tones contrast with the tawny head and body that are characteristic of *O. talamancae* as well as with its bright

Fig. 53. Contrast in vibrissal lengths between *Oryzomys bolivaris* (**left**; based on MSB 45826 and USNM 306924) and *O. talamancae* (**right**; drawn from AMNH 62034 and 66229). Note the extremely long superciliary (originating above the eye) and genal (behind the eye) vibrissae of *O. bolivaris* in comparison with those of *O. talamancae*.

tawny buff along sides of the body. The brighter tones result from the buffy tips of the overhairs, which are twice as long in *O. talamancae* as those of *O. bolivaris.* The distinction is obvious between adults but obscure between young adults, many of which cannot be separated on these chromatic features. Juveniles are also similar in fur coloration, but young *O. bolivaris* are darker and their coats are blackish with a slight brown suffusion; juvenile *O. talamancae* are olive-brown, often with pale yellow highlights.

The ventral coat of *O. bolivaris* is dark gray and contrasts with the bright whitish gray pelage typical of *O. talamancae.* In both species, the overhairs are gray in their basal portions and unpigmented distally but the whitish segments are shorter in *O. bolivaris* and longer in *O. talamancae.* The contrast between adults of each species is striking, but less distinct between young adults, and slight but noticeable between juveniles.

Tail: In addition to the differences in absolute and relative tail length between adults of the two species, tails of adult *O. bolivaris* are covered with smaller scales, as indexed by number of scales per centimeter. This distinction does not exist between available samples of each species in the three younger age categories (tables 27, 28).

We could not detect any differences between the two species in color or pigmentation pattern of the tails, at least in the samples from ‘‘Cerro Azul.’’ Certain darkly pigmented specimens of *O. bolivaris* from outside of Panamá (Colombia, for example) have tails that are noticeably darker than those typical of *O. talamancae* from throughout its geographic range.

Hind feet: General conformation of the hind feet (elongate, with short outer digits, longer middle digits, moderately large plantar pads) is similar in samples of *O. bolivaris* and *O. talamancae.* The two species differ in details. *Oryzomys bolivaris,* as we noted above, has on average a longer foot (table 27). Hairs covering the dorsal surface of the

TABLE 27

Descriptive Statistics for Measurements (mm) of Adult and Young Adult *Oryzomys bolivaris* and *Oryzomys talamancae* Collected at "Cerro Azul," Panamá

(Mean, ± 1 SD, observed range in parentheses, and number of specimens in sample are listed for each measurement. *P* is the level of probability derived from a table of cumulative Student's *t* distribution; values less than 0.05 [in boldface] were considered significant to reject the hypothesis that means of any two samples were drawn from the same population. Specimens measured are identified in footnotes.)

	Adults			Young adults		
	O. bolivaris[a]	*P*	*O. talamancae*[b]	*O. bolivaris*[c]	*P*	*O. talamancae*[d]
LHB	120.6 ± 10.8 (106–140) 9	0.8–0.7	119.6 ± 6.1 (110–129) 15	114.7 ± 5.9 (105–123) 7	0.5–0.4	111.4 ± 8.0 (93–121) 5
LT	121.7 ± 6.2 (111–130) 9	**<0.001**	130.7 ± 7.1 (115–146) 22	116.8 ± 7.5 (109–127) 5	0.9–0.8	117.6 ± 10.5 (108–135) 5
LHF	30.7 ± 1.8 (27–33) 9	**<0.001**	28.5 ± 1.6 (26–33) 26	29.1 ± 0.9 (28–30) 7	**0.02–0.01**	27.4 ± 1.4 (26–30) 7
LDF	10.4 ± 0.5 (10–11) 9	**<0.001**	8.2 ± 0.5 (7–9) 26	9.9 ± 1.5 (7–11) 7	**<0.001**	7.4 ± 0.5 (7–8) 7
LMV	48.9 ± 2.9 (45–54) 9	**<0.001**	34.6 ± 3.3 (28–41) 26	44.1 ± 5.3 (35–52) 7	**<0.001**	31.1 ± 1.9 (28–33) 7
LSV	56.4 ± 5.0 (46–65) 9	**<0.001**	30.2 ± 2.9 (26–35) 25	51.0 ± 7.1 (38–61) 7	**<0.001**	25.0 ± 1.9 (23–28) 7
LGV	35.9 ± 5.0 (28–43) 9	**<0.001**	17.3 ± 2.2 (13–21) 26	36.7 ± 3.6 (35–42) 7	**<0.001**	16.6 ± 2.2 (15–20) 7
TSR/CM	17.1 ± 2.8 (14–23) 9	**<0.001**	13.6 ± 1.2 (11–16) 23	17.8 ± 1.6 (16–20) 7	0.1–0.05	15.4 ± 2.4 (13–19) 5
ONL	31.2 ± 0.81 (30.3–32.5) 9	0.4–0.3	31.5 ± 0.83 (30.3–33.3) 24	29.2 ± 0.64 (28.1–29.8) 6	0.5–0.4	28.9 ± 0.70 (28.1–29.7) 4
ZB	15.3 ± 0.34 (14.8–15.9) 9	**0.05–0.02**	15.6 ± 0.37 (15.1–16.4) 24	13.9 ± 0.39 (13.4–14.5) 6	0.1–0.05	14.4 ± 0.29 (14.0–14.7) 4
IB	5.2 ± 0.15 (5.0–5.5) 9	**0.01–0.001**	4.9 ± 0.20 (4.6–5.3) 24	5.0 ± 0.06 (4.9–5.1) 6	0.1–0.05	4.8 ± 0.17 (4.6–5.0) 4
LR	9.7 ± 0.27 (9.3–10.1) 9	**0.02–0.01**	10.0 ± 0.44 (9.4–10.4) 24	9.1 ± 0.44 (8.3–9.5) 6	0.7–0.6	8.9 ± 0.36 (8.6–9.4) 4
BR	5.4 ± 0.15 (5.2–5.6) 9	**0.01–0.001**	5.7 ± 0.28 (5.3–6.4) 24	5.1 ± 0.15 (4.8–5.2) 6	0.4–0.3	5.2 ± 0.19 (4.9–5.3) 4
LB	11.8 ± 0.22 (11.5–12.1) 9	0.5–0.4	11.8 ± 0.32 (11.0–12.2) 24	11.4 ± 0.34 (11.0–12.0) 6	0.2–0.1	11.1 ± 0.22 (10.8–11.3) 4
HBC	8.6 ± 0.21 (8.3–8.9) 9	0.1–0.05	8.4 ± 0.25 (7.8–9.0) 24	8.2 ± 0.19 (8.0–8.5) 6	0.2–0.1	8.1 ± 0.17 (7.8–8.2) 4
BZP	3.0 ± 0.18 (2.7–3.3) 9	**0.05–0.02**	3.2 ± 0.23 (2.7–3.7) 24	2.8 ± 0.14 (2.5–2.9) 6	0.5–0.4	2.6 ± 0.10 (2.5–2.7) 4
LD	8.0 ± 0.24 (7.6–8.4) 9	0.2–0.1	8.2 ± 0.34 (7.7–8.9) 24	7.4 ± 0.29 (6.9–7.7) 6	0.5–0.4	7.2 ± 0.15 (7.0–7.3) 4
LBP	6.1 ± 0.46 (5.3–6.9) 9	**<0.001**	6.9 ± 0.36 (6.2–7.4) 24	5.8 ± 0.24 (5.4–6.1) 6	**<0.001**	6.5 ± 0.12 (6.4–6.6) 4
BBP	5.7 ± 0.20 (5.5–6.1) 9	—	5.7 ± 0.25 (5.2–6.3) 24	5.4 ± 0.12 (5.2–5.5) 6	0.4–0.3	5.5 ± 0.17 (5.3–5.7) 4

TABLE 27
(*Continued*)

	Adults			Young adults		
	O. bolivaris[a]	*P*	*O. talamancae*[b]	*O. bolivaris*[c]	*P*	*O. talamancae*[d]
PPl	10.5 ± 0.46 (10.0–11.3) 9	0.4–0.3	10.7 ± 0.50 (9.9–11.5) 24	9.5 ± 0.19 (9.3–9.7) 6	0.9–0.8	9.5 ± 0.65 (8.8–10.1) 4
LIF	4.8 ± 0.33 (4.4–5.6) 9	**0.05–0.02**	4.6 ± 0.33 (4.0–5.3) 24	4.4 ± 0.12 (4.2–4.5) 6	**0.01–0.001**	4.0 ± 0.24 (3.7–4.2) 4
BIF	2.3 ± 0.18 (2.1–2.6) 9	0.3–0.2	2.4 ± 0.15 (2.1–2.7) 24	2.3 ± 0.13 (2.1–2.5) 6	0.5–0.4	2.2 ± 0.18 (2.0–2.4) 4
CLM1–3	4.4 ± 0.12 (4.2–4.6) 8	0.1–0.05	4.5 ± 0.13 (4.3–4.8) 24	4.4 ± 0.10 (4.2–4.5) 6	0.2–0.01	4.6 ± 0.15 (4.4–4.7) 4
BM1	1.4 ± 0.05 (1.3–1.4) 9	**0.01–0.001**	1.3 ± 0.06 (1.2–1.4) 24	1.3 ± 0.05 (1.3–1.4) 6	—	1.3 ± 0.05 (1.3–1.4) 4

[a] USNM 171104, 171105, 306916–306918, 306920, 306921, 306924, 306925.

[b] USNM 302496–302499, 302501, 302503–302506, 302667, 302669–302677, 303103, 303104, 306953, 306954, 306956, 306958, 306959.

[c] USNM 171104, 305649, 305651, 305658, 306919, 306922, 306923.

[d] USNM 302493, 302500, 302502, 302668, 306955, 306957, 310569.

metatarsal region and digits are shorter than those in examples of *O. talamancae,* a contrast evident at all age categories of each species. The hairs of *O. talamancae* are long enough to extend beneath the foot and partially cover the plantar surface near the heel; this region in *O. bolivaris* is naked (fig. 54).

Cranium: Skulls of the two species are closely similar in shape (figs. 57–61) and overall size (indexed by occipitonasal length, zygomatic and lambdoidal breadths; tables 27, 28). Adults can be distinguished by a few quantitative and qualitative features. Our small samples of younger animals, however, especially juveniles and those in the transition between juvenile and adult pelages, are consistently separable by only one cranial trait.

Compared with adult *O. talamancae, O. bolivaris* of comparable age from ‘‘Cerro Azul’’ have on average a significantly narrower zygomatic breadth, a wider interorbit, a shorter and narrower rostrum, narrower zygomatic plate, much shorter bony palate, longer incisive foramina, and wider first upper molars (table 27). These absolute differences are also reflected in proportional contrasts. Relative to occipitonasal length, for example, the interorbit is significantly wider, the incisive foramina shorter, the rostrum and zygomatic plate narrower, and the bony palate much shorter (fig. 52).

Results of a principal components analysis (fig. 55) also highlight the same differences revealed by univariate statistical analyses of mean values of the adult samples. Covariation in lengths of bony palate and incisive foramina and in breadths of rostrum and zygomatic plate are primarily responsible for the two slightly overlapping specific clusters along the first principal component (table 29). The specimen of *O. bolivaris* (identified by arrow) nestled within the cluster of *O. talamancae* has the longest palatal bridge of any *O. bolivaris* we measured. No discrimination between the two species is apparent along the second principal component. Variation in shape of the incisive foramina (length and breadth) is primarily responsible for the dispersion of scores along that axis. Partial segregation does exist along the third component and it mostly reflects the difference in molar breadth between adults of the two species.

There is less mensural distinction between samples of the two species in the three youngest age groups; crania from each species in these age categories are difficult to separate by measurement alone. Thus, young animals are the specimens most often incorrectly

TABLE 28

Descriptive Statistics for Measurements (mm) of Young Adult–Juvenile and Juvenile *Oryzomys bolivaris* and *Oryzomys talamancae* Collected at "Cerro Azul," Panamá

(Mean, ± 1 SD, observed range in parentheses, and number of specimens in sample are listed for each measurement. *P* is the level of probability derived from a table of cumulative Student's *t* distribution; values less than 0.05 [in boldface] were considered significant to reject the hypothesis that means of any two samples were drawn from the same population. Specimens measured are identified in footnotes.)

	Young adults–Juveniles[a]			Juveniles[b]		
	O. bolivaris[c]	*P*	*O. talamancae*[d]	*O. bolivaris*[e]	*P*	*O. talamancae*[f]
LHB	102.6 ± 5.4 (94–110) 7	0.8–0.7	101.0 ± 12.7 (92–110) 2	78		89.0 ± 5.0 (82–93) 4
LT	102.0 ± 7.7 (90–107) 5	0.6–0.5	98.5 ± 2.1 (97–100) 2	75		82.8 ± 4.2 (77–87) 4
LHF	27.1 ± 1.5 (26–30) 7	0.6–0.5	26.5 ± 0.7 (26–27) 2	23		24.5 ± 1.3 (23–26) 4
LDF	6.9 ± 0.9 (6–8) 7	—	5.0 ± 0.0 (—) 1	6		5.3 ± 0.5 (5–6) 4
LMV	41.4 ± 4.0 (36–47) 7	**0.02–0.01**	31.5 ± 0.7 (31–32) 2	28		24.0 ± 1.4 (22–25) 4
LSV	48.0 ± 5.0 (40–55) 7	**<0.001**	25.0 ± 0.0 (—) 2	28		23.3 ± 4.4 (19–27) 4
LGV	28.7 ± 2.2 (25–31) 6	**<0.001**	16.0 ± 1.4 (15–17) 2	—		—
TSR/CM	20.0 ± 3.2 (16–24) 6	0.4–0.3	17.5 ± 2.1 (16–19) 2	—		—
ONL	26.6 ± 0.84 (25.5–27.5) 6	0.3–0.2	27.5 ± 0.35 (27.2–27.7) 2	24.8 ± 1.12 (23.5–25.6) 3	0.9–0.8	24.6 ± 0.59 (23.8–25.1) 4
ZB	12.9 ± 0.57 (12.2–13.7) 7	**0.05–0.02**	13.5 ± 0.07 (13.4–13.5) 2	12.3 ± 0.32 (11.9–12.5) 3	0.5–0.4	12.4 ± 0.22 (12.2–12.7) 4
IB	4.9 ± 0.11 (4.8–5.1) 7	0.8–0.7	4.8 ± 0.0 (—) 2	4.7 ± 0.06 (4.7–4.8) 3	0.1–0.05	4.5 ± 0.13 (4.4–4.7) 4
LR	7.8 ± 0.41 (7.5–8.7) 7	0.1–0.05	8.5 ± 0.07 (8.4–8.5) 2	7.1 ± 0.29 (6.8–7.3) 3	0.4–0.3	7.4 ± 0.43 (6.8–7.7) 4
BR	4.6 ± 0.13 (4.5–4.9) 7	**0.02–0.01**	5.0 ± 0.14 (4.9–5.1) 2	4.5 ± 0.21 (4.3–4.7) 3	0.9–0.8	4.5 ± 0.14 (4.3–4.6) 4
LB	10.9 ± 0.22 (10.6–11.2) 6	0.2–0.1	11.4 ± 0.64 (10.9–11.8) 2	10.5 ± 0.26 (10.3–10.8) 3	0.4–0.3	10.3 ± 0.15 (10.2–10.5) 4
HBC	8.0 ± 0.21 (7.7–8.2) 6	0.2–0.1	7.7 ± 0.0 (—) 2	7.5 ± 0.12 (7.4–7.6) 3	0.5–0.4	7.4 ± 0.17 (7.2–7.6) 4
BZP	2.3 ± 0.08 (2.2–2.4) 7	0.9–0.8	2.4 ± 0.07 (2.3–2.4) 2	2.1 ± 0.17 (1.9–2.2) 3	>0.9	2.1 ± 0.20 (1.8–2.2) 4
LD	6.4 ± 0.26 (6.1–6.8) 7	**0.01–0.001**	7.2 ± 0.07 (7.1–7.2) 2	6.0 ± 0.44 (5.5–6.3) 3	0.5–0.4	6.2 ± 0.36 (5.7–6.5) 4
LBP	5.3 ± 0.15 (5.2–5.6) 6	**0.01–0.001**	5.9 ± 0.07 (5.8–5.9) 2	5.3 ± 0.21 (5.1–5.5) 3	0.2–0.1	5.6 ± 0.26 (5.3–5.9) 4
BBP	5.0 ± 0.09 (4.9–5.1) 6	0.6–0.5	5.1 ± 0.07 (5.0–5.1) 2	4.9 ± 0.10 (4.8–5.0) 3	0.3–0.2	5.0 ± 0.08 (4.9–5.1) 4

TABLE 28
(*Continued*)

	Young adults–Juveniles[a]			Juveniles[b]		
	O. bolivaris[c]	*P*	*O. talamancae*[d]	*O. bolivaris*[e]	*P*	*O. talamancae*[f]
PPL	8.3 ± 0.39 (7.8–8.7) 6	0.2–0.1	8.8 ± 0.14 (8.7–8.9) 2	7.4 ± 0.31 (7.1–7.7) 3	0.9–0.8	7.4 ± 0.20 (7.1–7.5) 4
LIF	4.0 ± 0.13 (3.8–4.2) 7	0.7–0.6	4.1 ± 0.07 (4.1–4.2) 2	3.6 ± 0.26 (3.3–3.8) 3	0.2–0.1	3.9 ± 0.17 (3.7–4.1) 4
BIF	2.2 ± 0.15 (2.0–2.4) 7	0.9–0.8	2.2 ± 0.0 (—) 2	2.0 ± 0.06 (2.0–2.1) 3	0.9–0.8	2.1 ± 0.13 (1.9–2.2) 4
CLM1–3	4.3 ± 0.14 (4.1–4.5) 7	0.6–0.5	4.3 ± 0.35 (4.0–4.5) 2	—		—
BM1	1.3 ± 0.0 (—) 7	0.1–0.05	1.2 ± 0.14 (1.1–1.3) 2	1.3 ± 0.06 (1.3–1.4) 3	0.3–0.2	1.3 ± 0.05 (1.2–1.3) 4

[a] Specimens in some stage of molt from juvenile to adult pelage.
[b] Specimens in full juvenile coat.
[c] USNM 305647, 305648, 305650, 305652, 305654, 305655, 305704.
[d] USNM 303102, 305703.
[e] USNM 305656, 305657, 305705. External measurements are from 305656 only, skins of the other two could not be located.
[f] USNM 323864, 323868, 323872, 323874.

identified in museum collections, particularly if represented only by skulls or skeletons. Still, the shorter palatal bridge and longer incisive foramina, which differ significantly between adult samples from "Cerro Azul", also differ significantly between young adult *O. bolivaris* and *O. talamancae* (table 27) as well as between specimens of those two species in the young adult-juvenile category (table 28). No significant differences in cranial or dental measurements exist between our two small samples of juveniles from "Cerro Azul" (table 28).

Results of a principal components analysis (fig. 56) reveal broad overlap between examples of *O. bolivaris* and *O. talamancae* when using adults and young adults from throughout their geographic ranges. No discrimination between the species is apparent along the first principal component. The spread of scores along this axis is strongly influenced by lengths of rostrum, diastema, postpalatal region, and bony palate—measurements reflecting size—as well as by breadths of rostrum and zygomatic plate (table 30). Most crania in these two samples cannot be separated by size alone. Structure is evident along the second principal component: two partially overlapping clouds of

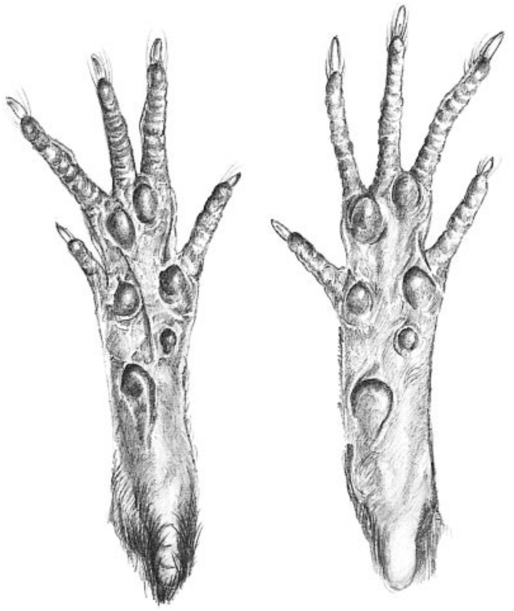

Fig. 54. Plantar surfaces of left hind feet from adult *O. talamancae* (**left**, AMNH 66229) and *O. bolivaris* (**right**, AMNH 45826). The area near the heel is exposed in samples of *O. bolivaris* but is partially concealed by fringes of hair in *O. talamancae*.

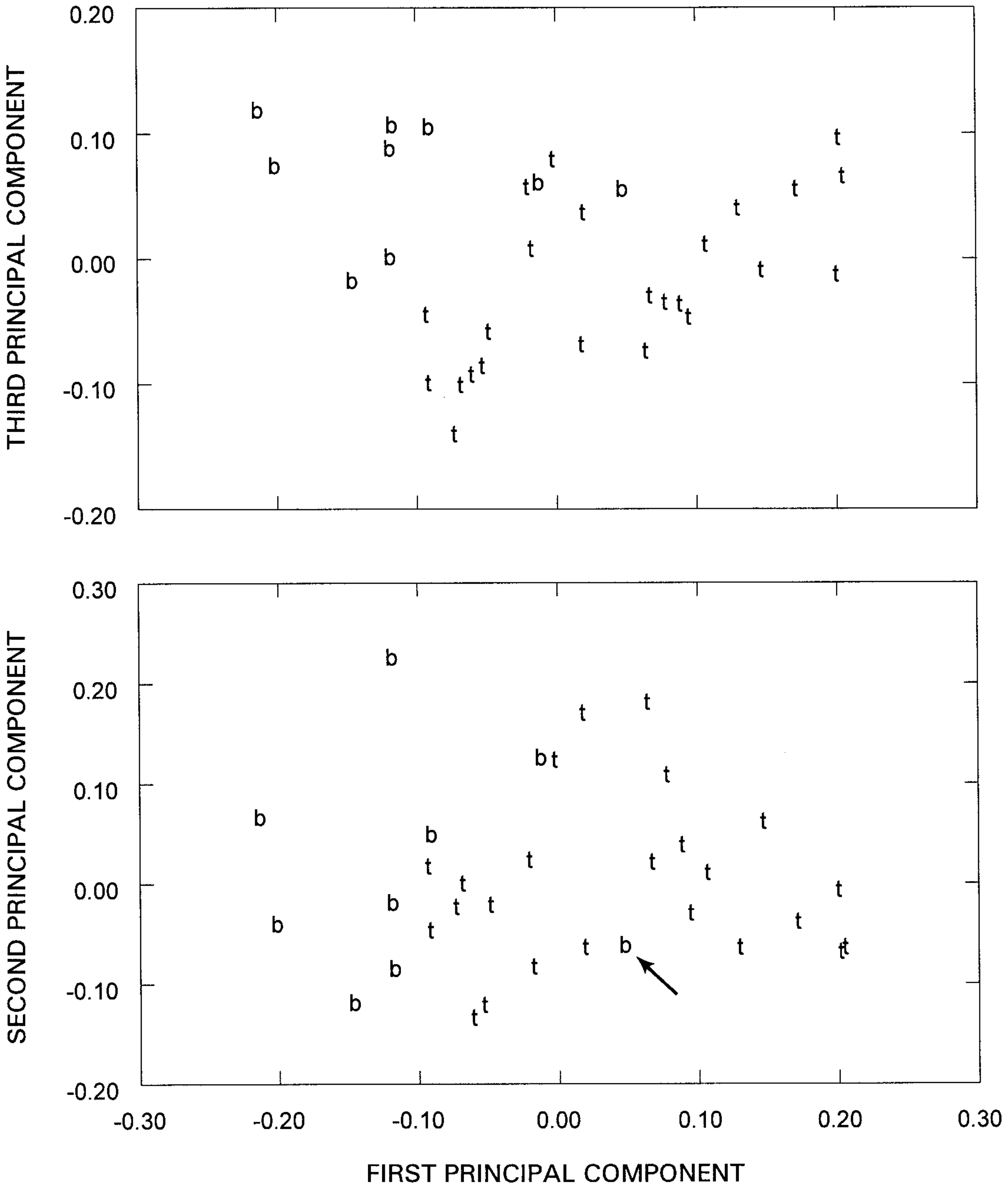

Fig. 55. Individual specimen scores based on log-transformed values of 14 cranial and 2 dental variables (see table 29) and projected onto the first and second and first and third principal components extracted from analysis of adult *Oryzomys bolivaris* (*N* = 9) and *O. talamancae* (*N* = 24) from "Cerro Azul," Panamá. Arrow identifies score representing a specimen of *O. bolivaris* with an exceptionally long bony palate, a trait characteristic of *O. talamancae* but otherwise exhibiting all the pelage, vibrissal, and parietal traits that are diagnostic of *O. bolivaris*. See discussion in text and summary statistics listed in table 27.

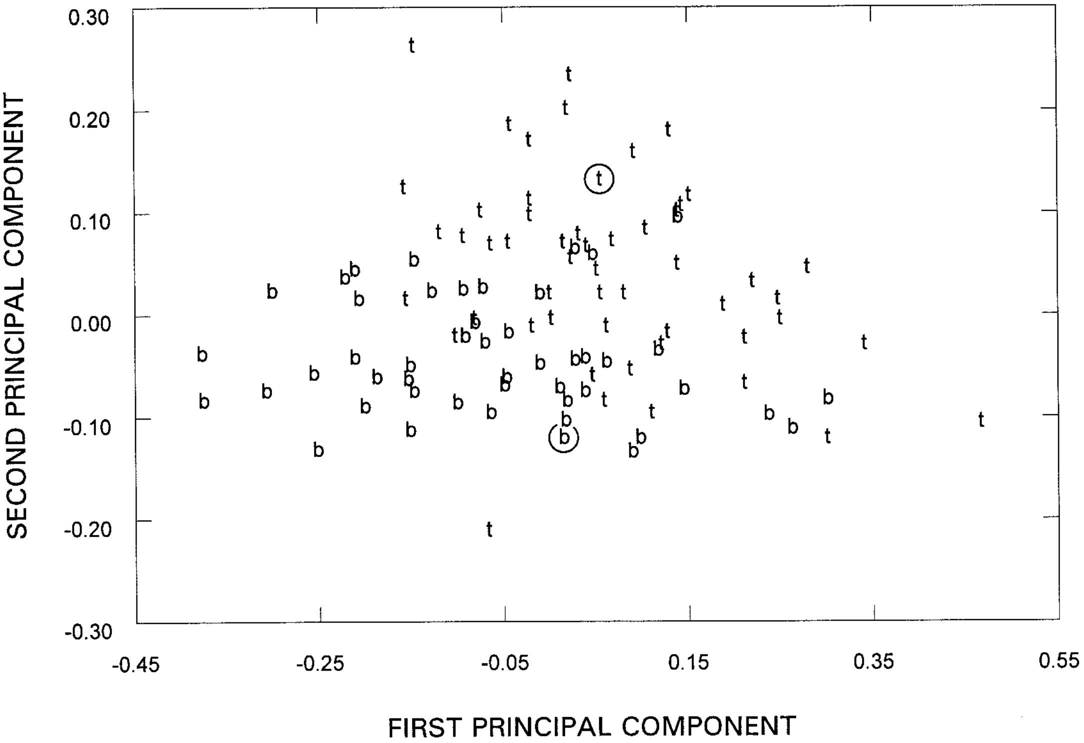

Fig. 56. Individual specimen scores based on log-transformed values of 12 cranial and 2 dental variables (see table 30) and projected onto the first and second principal components extracted from analysis of adult and young adult *Oryzomys bolivaris* (*N* = 49) and *O. talamancae* (*N* = 52). *Oryzomys bolivaris* is represented by specimens from Honduras, Nicaragua, Costa Rica, Panamá, Colombia, and Ecuador; examples of *O. talamancae* come from Costa Rica, Panamá, Colombia, and Ecuador. Scores representing holotypes of *O. bolivaris* (BMNH 99.9.9.27) and *O. talamancae* (USNM 12222/22742) are circled. Significance of the dispersal is discussed in text.

scores, which reflect results from univariate analyses of the samples from "Cerro Azul," emphasize the role of bony palate, and to a lesser degree, incisive foramina as cranial discriminators between adults and young adults of each species (table 28). Dispersion of scores along the third principal component (not illustrated), which primarily reflects variation in breadths of zygomatic plate and incisive foramina, does not discriminate between species.

Two qualitative traits of the skull provide contrasts, independent of age, between the species: the extent of the parietal below the temporal ridge and expression of the supraorbital ridges. In 84% of all examples of *O. bolivaris* examined, including nearly all from "Cerro Azul," the lateral margin of the parietal is defined by a distinct temporal ridge, below which the parietal does not extend nor contribute to the lateral braincase; 16% of the specimens exhibit a slight irregular projection of the parietal below the temporal ridge (table 31; fig. 62: character state 1). In contrast, of 606 examples of *O. talamancae,* almost all have a wing of the parietal that extends below the temporal ridge to form a minor or major portion of the braincase wall dorsal to the squamosal root of the zygomatic arch; only two specimens (less than 1%) lack the parietal as a component of the braincase wall.

The interorbital region is bordered by ridges in specimens of *O. bolivaris* and *O. talamancae,* but they are usually more conspicuous in the former because they are slightly higher and take the form of narrow shelves in many specimens. The difference can be

Fig. 57. Dorsal views of crania of *Oryzomys bolivaris* from ''Cerro Azul,'' Panamá, illustrating the four age categories described in text. From left to right: adult (USNM 306918), young adult (USNM 306923), young adult–juvenile (USNM 305647), juvenile (USNM 305705). Compare these views with those of *O. talamancae* in figure 58 on opposite page. ×3.

Fig. 58. Dorsal views of of crania of *Oryzomys talamancae* from Panamá, illustrating four age categories. From left to right: adult (USNM 306103), ''Cerro Azul''; young adult (USNM 306957), ''Cerro Azul''; young adult–juvenile (USNM 303102), ''Cerro Azul''; juvenile (USNM 323872), Cerro Hoya. Compare with views of *O. bolivaris* on opposite page, and see discussion in text. ×3.

Fig. 59. Ventral views of same crania of *Oryzomys bolivaris* shown in figure 57. Contrast these views with those of *O. talamancae* in figure 60 on opposite page. ×3.

Fig. 60. Ventral views of same crania of *Oryzomys talamancae* shown in figure 58. Contrast these views with those of *O. bolivaris* on opposite page. ×3.

TABLE 29

Results of Principal Components Analysis of Adult *Oryzomys bolivaris* and *Oryzomys talamancae* from "Cerro Azul," Panamá

(Component loadings most strongly influencing dispersion of scores are in boldface. Values are summarized statistically in table 27 and were obtained from the specimens listed in that table. See fig. 55.)

Variable	Principal components First	Second	Third
ONL	0.014	0.016	−0.001
ZB	0.017	0.009	0.003
IB	0.003	0.011	0.023
LR	0.015	0.011	−0.013
BR	**0.033**	0.020	−0.005
LB	0.004	0.010	0.001
HBC	0.003	0.006	0.010
BZP	**0.055**	0.015	0.024
LD	0.022	0.022	−0.007
LBP	**0.065**	−0.024	−0.028
BBP	0.023	0.017	0.027
PPL	0.027	0.028	0.009
LIF	**−0.050**	**0.047**	−0.012
BIF	0.002	**0.048**	−0.025
CLM1–3	0.009	0.005	0.004
BM1	0.015	0.001	**0.035**
Eigenvalue	0.014	0.008	0.005
% Variance	34.7	20.7	13.1

TABLE 30

Results of Principal Components Analysis of Adult and Young Adult *Oryzomys bolivaris* and *Oryzomys talamancae*

(Component loadings most strongly influencing dispersion of scores are in boldface. Specimens of *O. bolivaris* are from Honduras, Nicaragua, Costa Rica, Panamá, Colombia, and Ecuador; examples of *O. talamancae* are from Costa Rica, Panamá, Colombia, and Ecuador. See fig. 56.)

Variable	Principal components First	Second	Third
ONL	0.040	0.000	0.000
ZB	0.039	0.001	0.002
IB	0.008	−0.019	0.015
LR	**0.055**	0.010	−0.007
BR	**0.060**	0.003	−0.009
HBC	0.012	−0.011	0.004
BZP	**0.055**	−0.004	**0.062**
LD	**0.056**	−0.001	−0.013
LBP	**0.056**	**0.054**	−0.015
PPL	**0.050**	0.001	0.005
LIF	0.026	**−0.045**	0.005
BIF	**0.046**	**−0.048**	**−0.036**
CLM1–3	0.017	0.010	−0.003
BM1	0.009	−0.003	0.013
Eigenvalue	0.025	0.008	0.006
% Variance	46.3	14.9	11.5

appreciated only when examples of similar age of each species are compared. The more robust shelf-like supraorbital ridges are apparent on specimens of *O. bolivaris* in all four age categories, from juveniles to adults (figs. 57, 58).

Mandible: We noted only one consistent and conspicuous difference between the two species in mandibular morphology. Adult *O. bolivaris* have a more robust dentary because the ascending ramus is deeper than it is in the more gracile dentary from examples of *O. talamancae* of comparable age (fig. 61).

Molars: Lengths of maxillary molar rows are similar in the two species—no significant difference between samples of *O. bolivaris* and *O. talamancae* in any of the four age categories were detected (tables 27, 28). Breadth of first upper molar, however, differed significantly between adults but not between samples in the younger age assignments. Adult *O. bolivaris* have wider first molars, both in absolute value and also relative to length of toothrow or occipitonasal length (fig. 52).

Positions of primary cusps, lophs, mures, folds, and pits relative to one another are alike in samples of *O. bolivaris* and *O. talamancae.* In each second upper molar of both species, the paracone is separated from the anteroloph by a long paraflexus and from the mesoloph by a single small enamel-lined pit or fossette (designated a "median fossette" by Hershkovitz, 1993: 12), which presumably is the proximal remnant of the mesoflexus (figs. 29C, D; 63). In most other species of oryzomyines (*O. yunganus, O. alfaroi, O. nitidus,* for example; figs. 30, 63), an enamel partition divides the mesoflexus into a fossette between the paracone and protocone, and a distal channel (in some nestlings and juveniles, fig. 29A), or a distal fossette (in most adults, fig. 29B), between paracone and mesoloph.

In the second lower molar of *O. bolivaris*

Fig. 61. Lateral views of adult crania and dentaries of *Oryzomys* from ‘‘Cerro Azul’’, Panamá. Top: *O. bolivaris* (USNM 306918). Bottom: *O. talamancae* (USNM 306103). ×3.

and *O. talamancae*, a long hypoflexid separates the protoconid and median murid from the hypoconid and medial portion of the entoconid (fig. 30C). In some juveniles, this elongate hypoflexid extends across the middle of the tooth to the lingual side where it coalesces with a very short entoflexid to form a transverse furrow dividing the anterior pair of cusps from the posterior pair. In most other species of oryzomyines (*O. yunganus, O. alfaroi*, and *O. nitidus* are again examples; figs. 32, 64), the hypoflexid extends lingually only halfway across the molar between the protoconid and hypoconid, and is separated from an enamel-lined fossettid by the median murid (fig. 30A, B). The fos-

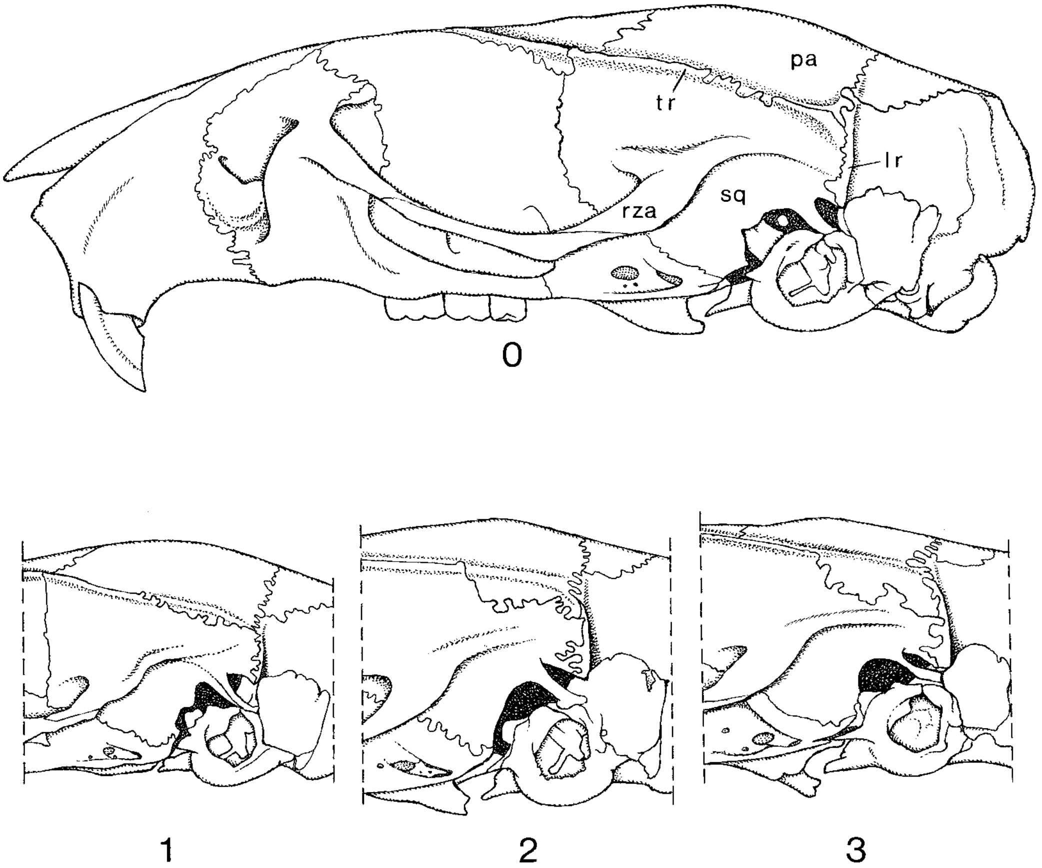

Fig. 62. Variation in contribution of the parietal to the lateral braincase wall in adult *Oryzomys bolivaris* (top) and *O. talamancae* (bottom sequence). In most examples of *O. bolivaris* (character state **0**, LSUMZ 26352 from Costa Rica), each lateral margin of the parietal (**pa**) is defined by a temporal ridge (**tr**); the braincase wall anterior to the lambdoidal ridge (**lr**) and dorsal to the root of the zygomatic arch (**rza**) is formed primarily by the squamosal (**sq**) (table 31). A contrasting arrangement characterizes nearly all specimens of *O. talamancae*: the braincase wall above the zygomatic root and anterior to the lambdoidal ridge consists of the squamosal and a ventral extension of the parietal. In the material surveyed, this ventral wing of the parietal may form a minor (**1**, AMNH 64811), moderate (**2**, AMNH 64828), or extensive (**3**, AMNH 64791) component of the wall above the zygomatic root (see table 31). Such a range in parietal extension can be found in most large samples of *O. talamancae* collected from the same locality (the three illustrated are from Cerro Manglar Alto, Ecuador).

sette is formed when lingual margins of the mesolophid and entoconid coalesce, separating the entoflexid into a medial fossettid and lingual crease.

Oryzomys bolivaris and *O. talamancae* also have the same number of roots anchoring each molar and resemble one another in molar shape (viewed from occlusal aspect) and overall size of one tooth relative to another.

Chromosomes: We do not have karyotypes of either *O. bolivaris* or *O. talamancae* from samples obtained at ‘‘Cerro Azul.’’ The only data available for each of the species come from Costa Rican specimens of *O. bolivaris* and Venezuelan and Ecuadoran series of *O. talamancae*. These contrast in diploid and fundamental numbers as well as the composition of biarmed and uniarmed autosomes (table 13).

TABLE 31
Variation of Lateral Parietal Extension Below the Temporal Ridge Among Adults of *Oryzomys bolivaris* and *Oryzomys talamancae*

Species and country	Extent of parietal below temporal ridge[a] 0	1	2	3
O. bolivaris				
Honduras	1	0	0	0
Nicaragua	1	4	0	0
Costa Rica	14	1	0	0
Panamá	32	4	0	0
Colombia	9	0	0	0
Ecuador	9	4	0	0
Total	66	13	0	0
O. talamancae				
Costa Rica	0	0	0	4
Panamá	1	13	237	48
Colombia	0	5	37	13
Venezuela	0	0	6	2
Ecuador	1	29	135	74
Total	2	47	416	141

[a] Character states coded 0 to 3 are illustrated and defined in figure 62.

Oryzomys bolivaris and *Oryzomys alfaroi*

External features: Examples of *O. bolivaris* are easily distinguished from specimens of *O. alfaroi* of comparable age by their larger body size (compare length of head and body and occipitonasal length from samples of *O. bolivaris,* table 25, with those of *O. alfaroi,* table 34), thicker and softer pelage, and much longer facial vibrissae. Texture and coloration of the dorsal fur and lengths of facial vibrissae relative to body size in samples of *O. alfaroi* are closely similar to examples of *O. talamancae.*

Cranium: A conspicuous cranial contrast between the two species, in addition to size, is the configuration of the parietal. The parietal extends below the temporal ridge in specimens of *O. alfaroi,* forming a pattern similar to that seen in *O. talamancae* (fig. 62). The suture formed by the parietal and squamosal is contained within the temporal ridge in examples of *O. bolivaris* and does not contribute to the lateral wall of the braincase.

Molars: *Oryzomys bolivaris* has longer molar rows (always exceeding 4.0 mm) than do specimens of *O. alfaroi* (usually shorter than 4.0 mm; contrast values in tables 25 and 34). Coronal patterns of the second upper and lower molars vary between the species (figs. 63, 64). In examples of *O. bolivaris,* the anterior margin of the paracone is bounded by a long, curved paraflexus, and the metaflexus on the posterior side of the cusp is represented by an enamel-lined pit or short trough, a configuration closely similar to that seen in specimens of *O. talamancae.* The paraflexus is short in *O. alfaroi* and is separated by an enamel partition from the mesoflexus, which is divided into two parts by an enamel partition. Like the second lower molar of *O. talamancae,* that of *O. bolivaris* is nearly divided into two sections by a long hypoflexid. In *O. alfaroi,* the hypoflexid extends only halfway across the molar, where it is separated by part of the median murid from a lingual fold, the entoflexid. This occlusal configuration, or something very similar to it, is typical of *O. yunganus* and several other kinds of oryzomyines (figs. 29–32).

Chromosomes: Chromosomal information is available for one sample of *Oryzomys bolivaris* and two of *O. alfaroi* (table 13). The two species differ in diploid and fundamental numbers: 2*n* of 58, FN of 80 for *O. bolivaris*; 2*n* of 60, FN of 104 for a sample of *O. alfaroi* from Veracruz, México (Haiduk et al., 1979); or 2*n* of 62, FN of 100 for a sample from Ecuador (fig. 71). The autosomal complement reported for the single sample of *O. bolivaris* from Costa Rica consists of 9 pairs of metacentrics and submetacentrics, 1 pair of subtelocentrics, and 16 pairs of telocentrics; the X is a subtelocentric and the Y a telocentric (table 13). The Mexican sample of *O. alfaroi* has 29 pairs of autosomes—23 pairs of metacentrics and submetacentrics and 6 pairs of telocentrics—and telocentric sex chromosomes. The sample of *O. alfaroi* from Ecuador consists of 16 metacentric or submetacentric pairs of autosomes, 4 subtelocentric pairs, and 10 telocentric pairs; a large subtelocentric and small telocentric form the sex chromosomes.

GEOGRAPHIC VARIATION AND SUBSPECIES

When Pine (1971) reviewed *O. bolivaris* under the name *bombycinus,* he evaluated the

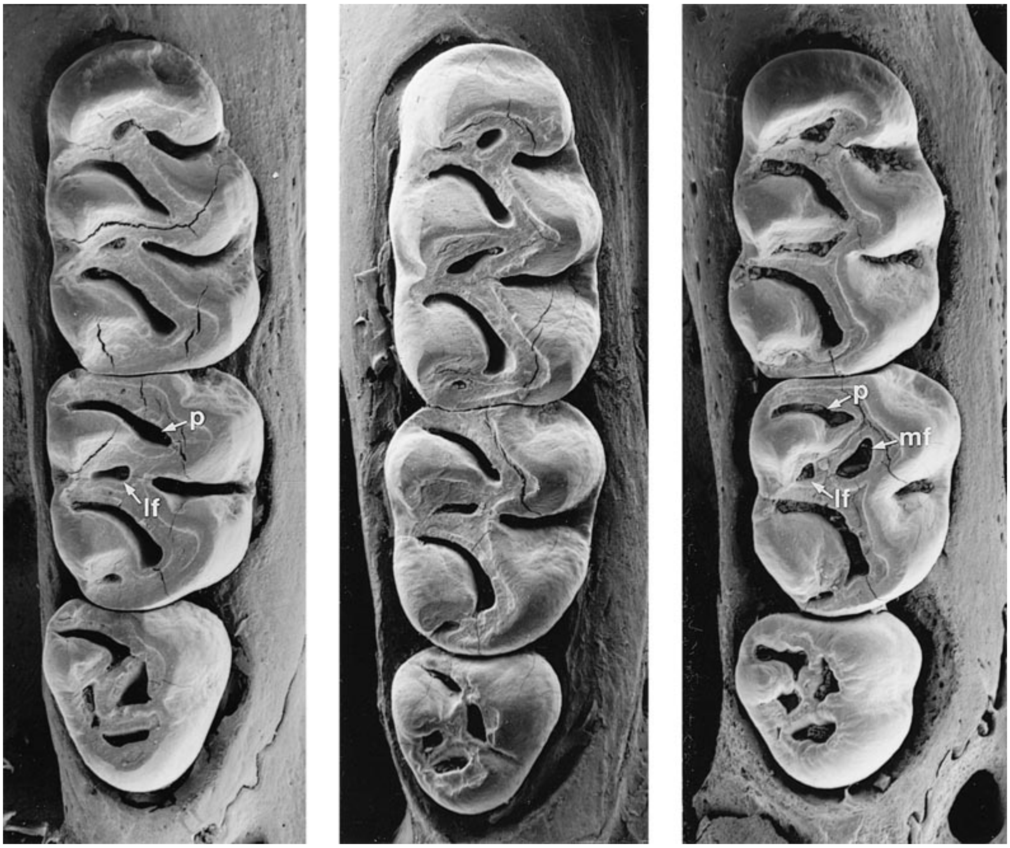

Fig. 63. Occlusal views of right upper molar rows from *Oryzomys*. **Left:** *O. talamancae* (AMNH 37922, Panamá; CLM1–3 = 4.5 mm). **Middle:** *O. bolivaris* (AMNH 7964/9624, Costa Rica; CLM1–3 = 4.2 mm). **Right:** *O. alfaroi* (AMNH 32878, Colombia; CLM1–3 = 3.9 mm). Each second molar of *O. bolivaris* and *O. talamancae* has a deep paraflexus (**p**) and labial fossette (**lf**), elements of a pattern contrasting with that of *O. alfaroi* in which a short paraflexus and two fossettes—labial and medial (**mf**)—are typical. See discussion in text and figures 29 and 30.

characters that had been used to distinguish the three subspecies recognized at the time (as listed in Hall and Kelson, 1959, and Handley, 1966, for example): *O. b. alleni* (Costa Rica, western Panamá), *O. b. bombycinus* (central Panamá), and *O. b. orinus* (eastern Panamá). Slight differences in dimensions of the skull and the degree of supraorbital ridging were employed by Goldman (1918:78) to separate *alleni* from typical *bombycinus*. These same cranial traits along with chromatic distinctions were cited by Pearson (1939) to define *orinus.*

Very few specimens of *bombycinus* were available to Goldman and Pearson. Goldman (1918), in his revision of North American *Oryzomys,* studied four *alleni* from Costa Rica and four typical *bombycinus* from Panamá. Three of the four from Costa Rica comprised the type series of *alleni*—two of these are juveniles and the holotype is a young adult. Four additional specimens, all old adults obtained by Pearson (1939) in eastern Panamá, were added to this meager representation of the species and formed the series upon which he based his description of *orinus.* Even minor morphological differences between such small samples, which are dissimilar in range of age variation and were gathered over such an extensive geographic region, seemed to loom large and significant.

By 1971, Pine was able to document 57 specimens of *O. bombycinus,* of which 29 represented nominal *bombycinus* from cen-

Fig. 64. Occlusal views of right lower molar rows from same specimens of *Oryzomys* illustrated in figure 63. **Left:** *O. talamancae* (clm1–3 = 4.9 mm). **Middle:** *O. bolivaris* (clm1–3 = 4.4 mm). **Right:** *O. alfaroi* (clm1–3 = 4.1 mm). Each second molar of *O. talamancae* and *O. bolivaris* has a deep hypoflexid (**h**) and shallow, creaselike entoflexid (**ef**). In contrast, the hypoflexid extends only to midline of the second molar in *O. alfaroi* (as seen in occlusal plane); its lingual counterpart, the entoflexid, has been closed by occlusion of lingual margins of mesolophid (**m**) and entoconid (**ec**) and is represented by a fossettid (**f**) and crease (**ef**) on the lingual surface of the molar. See discussion in text and figures 31 and 32.

tral Panamá, and 27 of these had been collected by either Goldman or Handley (1966: 780) on ‘‘Cerro Azul’’ (Cerro Prominente and La Zumbadora, locality 19 in gazetteer). Pine’s (1971) evaluation of variation in cranial traits within the sample from ‘‘Cerro Azul’’ led him to reject the cranial characters held to be diagnostic for *alleni* or *orinus* as insignificant indicators of different populations; instead he attributed the supposed differences to sampling artifacts (small samples, unequal ranges in age). The variation in cranial traits among all the samples, in Pine’s view, was not significant in the detection and definition of geographic subgroups within *O. bombycinus.*

Variation between particular samples in color of fur did impress Pine, for he used chromatic differences to distinguish the three subspecies recognized. Samples called *alleni* from Nicaragua, Costa Rica, and western Panamá were ‘‘distinguished from the geographically adjacent subspecies, *O. b. bombycinus* [central Panamá] by darker coloration’’ (Pine, 1971: 591). Compared with typical *bombycinus,* samples of *orinus* from eastern Panamá, Colombia, and Ecuador were darker and had richer tones in the dorsal coat. In Pine's assessment, the fur in the sample from central Panamá was not as dark or richly pigmented as was the pelage in samples from geographic regions to the west or east. He remarked that "*O. b. alleni* differs from *O. b. bombycinus* in the same ways as does *O. b. orinus*; if *alleni* and *orinus* had adjacent geographic ranges, instead of being separated from each other by the range of *bombycinus,* I would make no taxonomic distinction between the two" (p. 592).

We examined the same specimens studied by Pine as well as 47 other examples. Even with these additional samples, however, we acknowledge the same problem that confronted Pine in attempting to assess the significance of morphometric and chromatic variation observed among the geographic series. Sampling has been historically uneven, with nothing available from extensive regions of several countries (see the map in fig. 50). Except for the ample series of 27 specimens from "Cerro Azul" in central Panamá, other samples are small and unequal in both number of specimens and composition of age and sex. For example, 19 of 36 gazetteered localities are represented by only one specimen, 4 other sites have two examples, 4 more places have three, and 8 are represented by from four to six. We pooled small locality samples to obtain reasonable summary statistics for comparison of measurement values (table 25).

Our qualitative observation of variation in cranial traits among the samples supports Pine's contention that this variation does not reflect significant distinctions among geographic subsets of *O. bolivaris.* Neither cranial nor dental traits define the three subspecies as outlined by Pine or delimit some other geographic pattern. Only slight differences exist between means of the cranial and dental measurements listed in table 25. For example, length of molar row, which is not affected by ontogenetic growth, is nearly identical in means from sample to sample.

The series from Colombia is an apparent exception to the close correspondence of cranial size among the samples. Certain cranial measurements (occipitonasal length, length and breadth of rostrum and bony palate, lengths of diastema and postpalatal region) average larger than those for the other samples. The significance of these differences will have to be tested by more and larger samples from Colombia and elsewhere.

TABLE 32

Results of Principal Components Analysis of Adult *Oryzomys bolivaris*

(Component loadings most strongly influencing dispersion of scores are in boldface. Specimens, which include the six holotypes, are from Honduras, Nicaragua, Costa Rica, Panamá, Colombia, and Ecuador. See fig. 65.)

	Principal components		
Variable	First	Second	Third
ONL	0.043	0.003	0.004
ZB	0.038	0.009	−0.001
IB	0.029	−0.010	0.005
LR	**0.049**	0.015	0.004
BR	**0.054**	0.004	0.001
LB	0.024	−0.007	−0.001
HBC	0.012	0.000	−0.004
BZP	**0.075**	**−0.039**	0.002
LD	**0.050**	0.017	0.012
LBP	**0.044**	−0.006	**0.033**
BBP	0.032	0.000	−0.005
PPL	**0.056**	0.003	−0.002
LIF	0.023	**0.043**	−0.021
BIF	0.039	−0.011	**−0.050**
CLM1–3	0.010	0.009	0.002
BM1	0.014	**0.039**	0.009
Eigenvalue	0.027	0.006	0.004
% Variance	53.4	11.8	8.8

Our perception of negligible geographic variation in cranial features, derived from summary statistics and simple inspection of skulls, is reinforced by principal components analysis (fig. 65) of specimens from throughout the geographic range of *O. bolivaris.* The general dispersion of scores along the first component is primarily influenced by variation in lengths of rostrum, diastema, bony palate, postpalatal length, and breadths of rostrum and zygomatic plate (table 32). The three scores isolated from the main cluster represent exceptionally large adults from Colombia and Ecuador and an old adult from Nicaragua.

Two clusters are weakly suggested along the second principal component, a dispersion heavily influenced by variation in breadths of zygomatic plate and first upper molar as well as length of incisive foramina. What signifi-

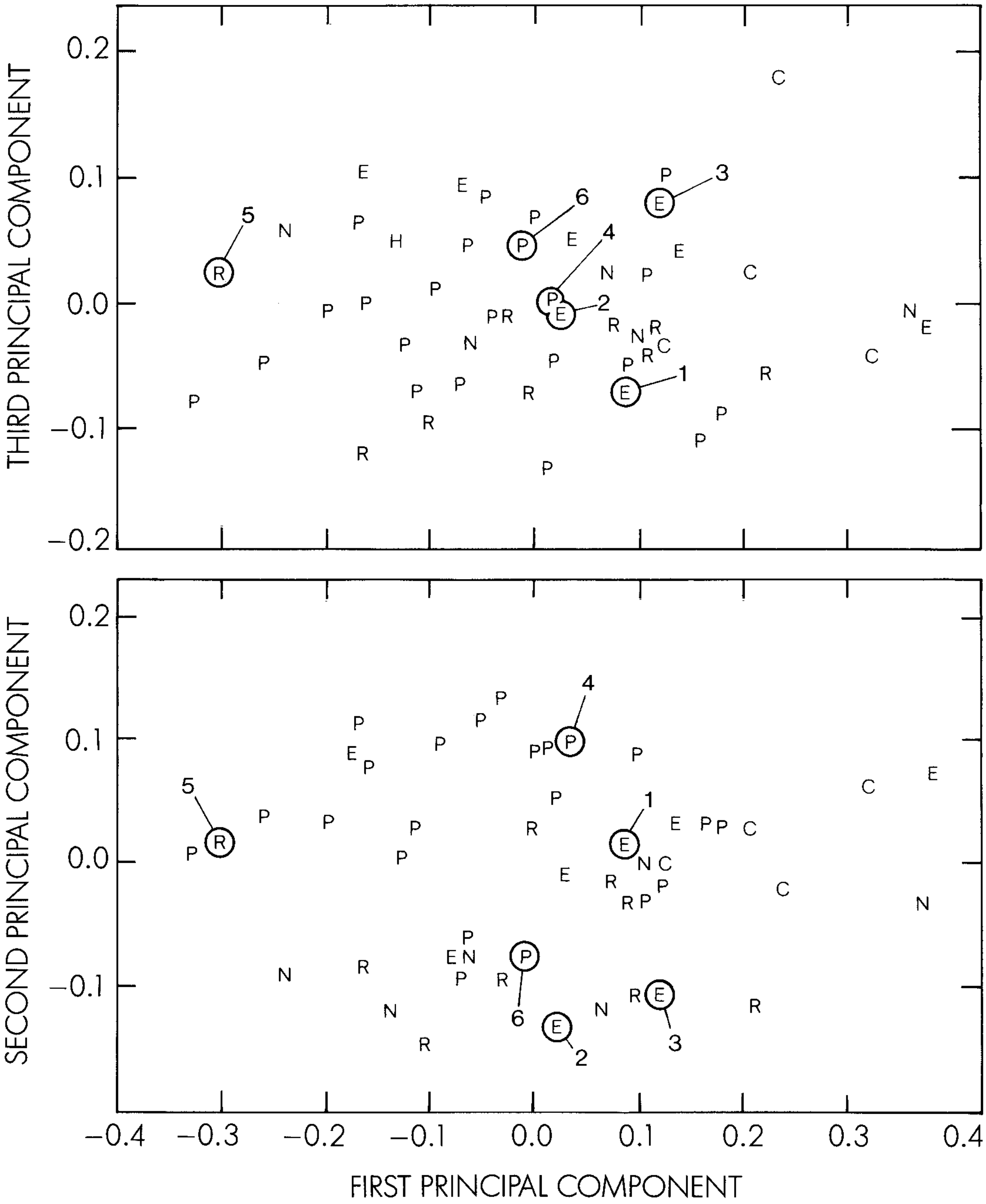

Fig. 65. Individual specimen scores based on log-transformed values of 14 cranial and two dental variables (see table 32) and projected onto the first and second and first and third principal components extracted from analysis of young to old adult *Oryzomys bolivaris* (*N* = 49). Letters identify specimens from Honduras (H), Nicaragua (N), Costa Rica (R), Panamá (P), Colombia (C), and Ecuador (E). Holotypes are represented by numbers: 1, *bolivaris* (BMNH 99.9.9.27); 2, *castaneus* (BMNH 1.3.19.11); 3, *rivularis* (BMNH 1.1.6.5); 4, *bombycinus* (USNM 171105); 5, *alleni* (AMNH 9631/7971); 6, *orinus* (ANSP 19709). Pattern formed by the scores is interpreted in text.

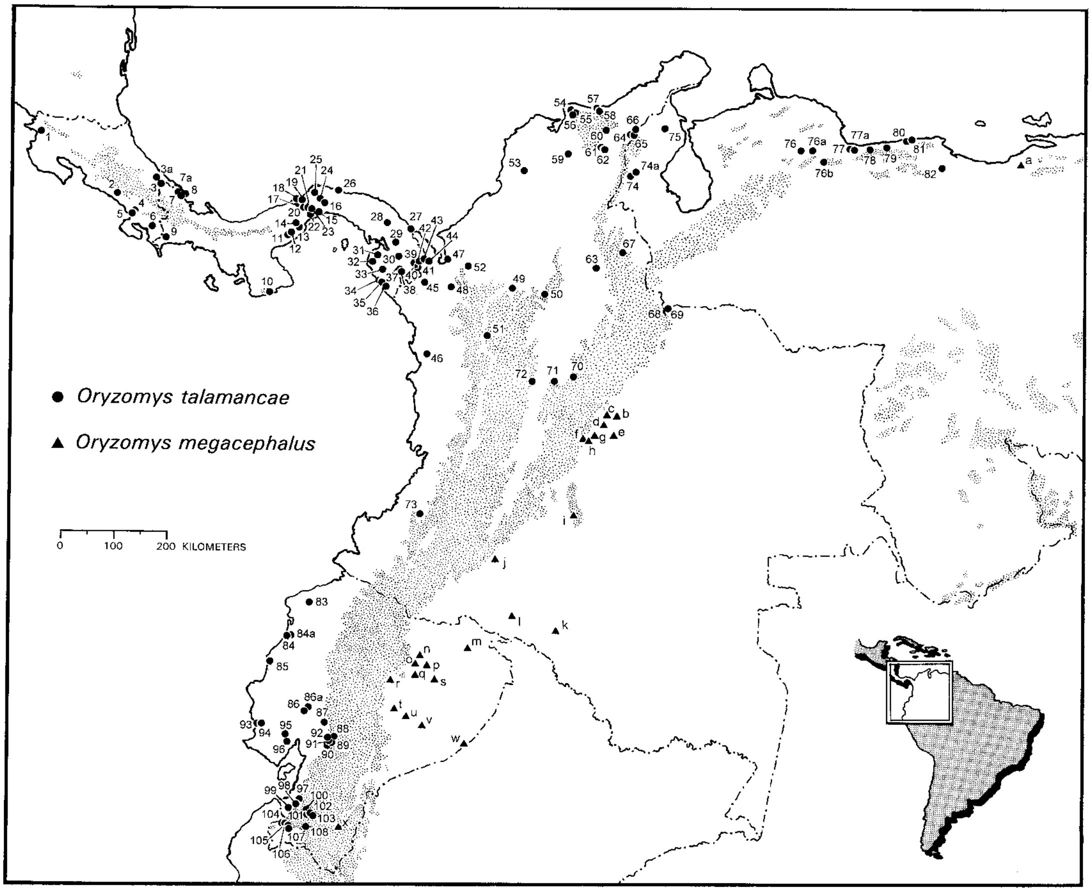

Fig. 66. Distributions of *Oryzomys talamancae* (based on collection localities [**1–108**] for 946 specimens examined) and *O. megacephalus* (localities **a–x**) from the western margin of its range in Ecuador, Colombia, and Venezuela. Numbers key to localities in gazetteers for each species where locality information is provided; specimens are identified by museum initials and catalog numbers. Stippling denotes areas above 1000 m.

cance this pattern heralds is unknown. Separation due to different age groups is not reflected because the range in age from young adults to old adults characterizes both clusters, and geographic pattern is not indicated because each cluster contains scores representing specimens obtained across the geographic range of *O. bolivaris.*

Dispersion along the third principal component resulted in one large cluster without significant structure—no geographic pattern, for example, is evident.

Coloration of fur varies within and among samples, but we could not detect any pattern that made sense with regard to geographic distribution. Animals with dark fur thought to be characteristic of *alleni* and *orinus* are found in the same sample as those with paler tones (this range of variation can be seen in the large series from ‘‘Cerro Azul’’). The few specimens from Colombia again provide an exception. Some are partially melanistic, as we noted above; however, the nonmelanistic adult coats closely resemble those in the series from ‘‘Cerro Azul.’’

By using the generally small samples available from widely scattered localities, we cannot detect any meaningful morphometric or chromatic variation that holds biogeographic significance. Rigorous definition of geographic units within the species is not possible with the material available for study,

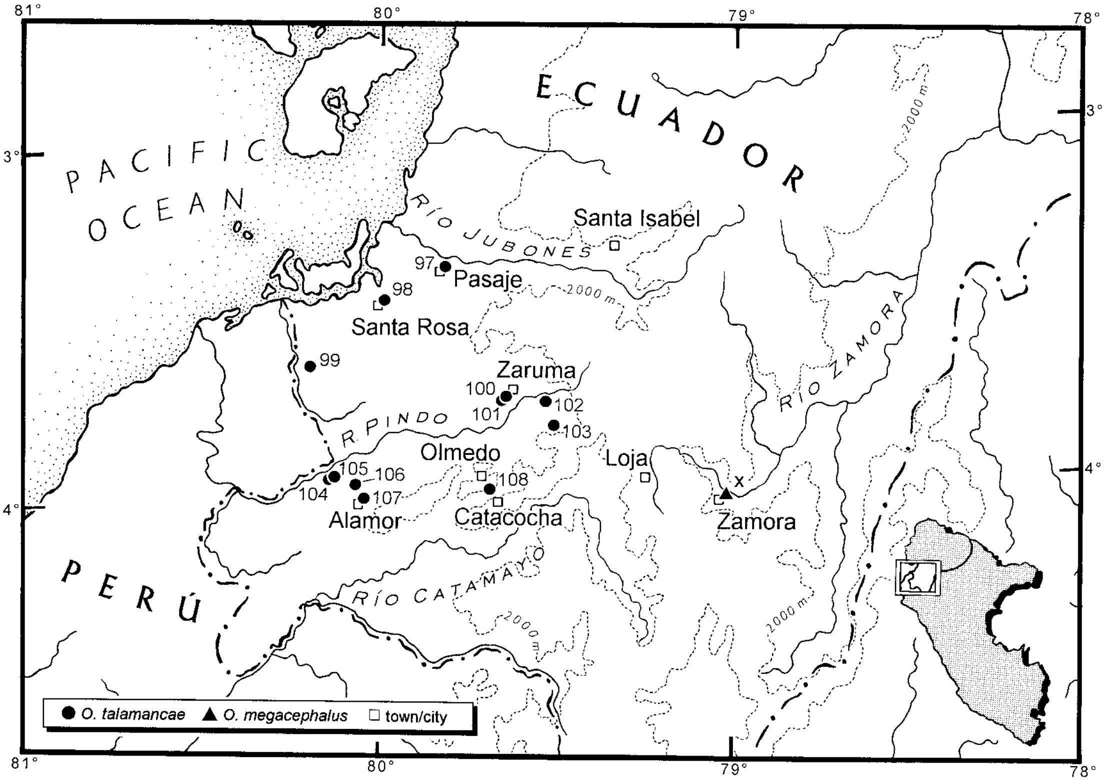

Fig. 67. Distribution of collection localities for *Oryzomys talamancae* (**97–108**) and *O. megacephalus* (**x**) in southern Ecuador. Numbers key to numbered localities in gazetteer for *O. talamancae*; locality **x** for *O. megacephalus* is origin of sample 11 in table 1. See discussion in text.

and for now we regard *O. bolivaris* as monotypic.

ORYZOMYS TALAMANCAE Allen, 1891

This species was recently reviewed by Musser and Williams (1985), and we present new information that enhances their account. First, we report additional collection localities of specimens not available to Musser and Williams, omit four specimens of *O. bolivaris* they misidentified as *O. talamancae,* and provide a revised gazetteer that contains better descriptions of localities and corrections of some latitudinal and longitudinal coordinates.

Second, we report variation in karyotypes from northern Venezuela and document chromosomal characteristics for two sets of samples from western Ecuador. These data are important to an understanding of chromosomal variation within *O. talamancae* and its significance for reconstructing the zoogeographic history of the species. Except for Venezuelan samples reported on by Pérez-Zapata et al. (1986), we know of no other published descriptions of karyotypes of *O. talamancae.*

Finally, we contrast *O. talamancae* with *O. alfaroi* and *O. megacephalus.* Specimens of the first two are similar enough in their morphology that they are often misidentified in museum collections. *Oryzomys talamancae,* once considered as conspecific with *O. megacephalus* (*capito* in older publications), is now treated as distinct, but contrasts in geographic distributions, morphology, and chromosomes have not been presented adequately in the literature.

GAZETTEER AND SPECIMENS

Collection localities for the 946 specimens of *Oryzomys talamancae* we studied are listed below. The number preceding each locality keys to a symbol on the map in figure 66. Only specimens we personally examined are recorded.

COSTA RICA

Provincia de Guanacaste

1. **Parque Nacional Santa Rosa**, which ‘‘is in northern Guanacaste Province, between the Golfo de Papagayo and the Inter-American Highway, with geographical coordinates 10°45′ to 11°00′N and 85°30′ to 85°45′W’’ (Hartshorn, 1983a: 125), 300 m: USNM 562178 (trapped in northwest portion of Parque).

Provincia de San José

2. **34.7 km SE (by road) San Isidro**, 09°15′N/83°30′W, 525 m: MVZ 164878, 164879.

Provincia de Limón

3. **Talamanca** (location is discussed in Taxonomic Summary), 09°32′N/82°55′W: USNM 25976 (holotype of *Oryzomys carrikeri*), 25974, 25975; USNM 12222/22742 (holotype of *Oryzomys talamancae*), 12227.

3a. **Estrella Valley, Pandora** (‘‘a town on the Río Estrella 11 km from the Atlantic Coast,’’ McPherson, 1985: 262), 09°43′N/82°57′W: USNM 284656. **Estrella Valley, Fortuna, 8 mi W Pandora**, 09°44′N/82°58′W: USNM 284657.

Provincia de Puntarenas

4. **Boruca,** which is ‘‘near the Río Diquis (= Río Grande de Térrabas), about 12 miles from the Pacific coast, altitude 1600 feet’’ (Goodwin, 1946: 454), 09°00′N/83°19′W (USBGN Costa Rica, 1983: 12): MCZ 12303.
5. **El Palmar,** which is a ‘‘hamlet on the Río Diquis, 9 miles from the Pacific coast, altitude 250 feet’’ (Goodwin, 1946: 456); El Palmar is now called Palmar Sur, 08°58′N/83°27′W, and the river is currently known as Río Grande de Térrabas (USBGN Costa Rica, 1983: 83; also see McPherson, 1985: 263): AMNH 139426–139428; LSUMZ 11518.
6. **Pan American Highway, 3.7 mi N Villa Neily,** 08°38′N/82°57′W, 50–100 m (McPherson, 1985: 271): LACM 25578.

PANAMÁ

(Unless indicated otherwise, coordinates are from Fairchild and Handley, 1966.)

Provincia de Bocas del Toro

7. **Almirante, 10 km NW,** 09°18′N/82°24′W (for Almirante), 1000 ft: USNM 293127, 293128, 315991.

7a. **Río Changuinola,** 09°22′N/82°31′W, 1000 ft: USNM 464510.

8. **Boca del Drago**, 09°26′N/82°20′W, 1000 ft: USNM 315992, 315995.

Provincia de Chiriquí

9. **Divalá**, 08°25′N/82°43′W: MCZ 10034

Provincia de Los Santos

10. **Cerro Hoya,** 07°18′N/80°42′W, 3000 ft: USNM 323864–323869, 323871–323879, 323912–323922.

Provincia de Coclé

11. **El Valle,** 08°36′N/80°08′W, 2000-3000 ft: USNM 303430, 304804.
12. **6 mi E El Valle,** 2000–3000 ft: USNM 304803, 304805–304808, 304811, 304812.

Provincia de Panamá

13. **Cerro Campana,** 08°41′N/79°56′W, 3000 ft: USNM 298716, 302673, 303421–303429, 304802.
14. **Maxon Ranch** (= Río Trinidad; see Anthony, 1916), 08°57′N/80°00′W: AMNH 36794, 36797, 36798.
15. **Sabanas, a suburb of Panamá** (= Panamá City; see Fairchild and Handley, 1966: 19), 08°58′N/79°52′W: BMNH 0.5.1.66, 0.5.1.67 (holotype of *Oryzomys panamensis,* ‘‘City of Panama’’).
16. **‘‘Cerro Azul,’’** which is the name on skin labels of specimens collected by C. O. Handley, Jr. from **La Zumbadora,** 09°14′N/79°21′W (see Fairchild and Handley, 1966: 18–19), 2500–3500 ft: USNM 302493, 302496–302506, 302567, 302674-302677, 303102–303104, 303260, 303261, 305703, 306952–306955, 306957, 306959, 310568, 310569, 310571–310574.

Provincia de Canal Zone

17. **Gatún**, 09°15′N/79°56′W: USNM 170978–170983.
18. **Fort Sherman, 6 mi W Cristóbal,** 09°21′N/79°57′W, 5 m: USNM 457264–457319. **Mohinga Valley, 3 mi S Fort Sherman**, 5 m: USNM 296304.
19. **Fort Gulick**, 09°18′N/79°53′W: USNM 396457.
20. **Barro Colorado Island,** 09°09′N/79°51′W: MCZ 30747, 30749.
21. **Buena Vista Peninsula, 1–2 km NW Frijoles,** 09°10′N/79°49′W: USNM 503717.
22. **Rodman Naval Station, 8 km W Balboa,** 08°56′N/79°35′W, 50 m: USNM 457230–457262.
23. **Madden Road,** ‘‘extending between Paraíso and Madden Dam, and passing through Madden Forest’’ (Fairchild and Handley, 1966: 14): USNM 300342–300344, 300346–300351, 301168–301170.
24. **Salamanca Hydrographic Station,** which is near Río Pequení, 09°17′N/79°35′W: MCZ 34308.

Provincia de Colón

25. **Cerro Bruja,** 09°29′N/79°34′W, 100 ft: USNM 171530.

Provincia de San Blas

26. **Mandinga**, 09°29′N/79°05′W: USNM 305645, 305646, 305699, 305700, 305702.
27. **Armila, Quebrada Venado,** 08°40′N/77°27′W: USNM 335567–335630.

Provincia de Darién

28. **Sante Fé,** 08°51′N/77°55′W: FMNH OICS No. 2556; MSU 15296. **Morti Hydro**: FMNH OICS No. 43556.
29. **Río Chucunaque**, 08°23′N/77°49′W: USNM 306960, 306961.
30. **El Real** (= Real de Santa María; see Anthony, 1916), 08°06′N/77°45′W: AMNH 37584.
31. **Río Esnápe,** 08°05′N/78°13′W: MCZ 19836.
32. **Cerro (Mount) Sapo,** 07°58′N/78°22′W, 1000–3000 ft: MCZ 39723.
33. **Pelisa** (on Río Pavarando?): ANSP 19710, 19711.
34. **Punta Piña**, 07°34′N/78°13′W: USNM 314727–314729, 324959, 396458–396463.
35. **Jaqué,** 07°31′N/78°10′W: USNM 363201–363216. **Amayal,** which is near Jaqué: ANSP 19726–19728.
36. **Guayabó**, 07°23′N/78°02′W: ANSP 19693–19700, 19713–19723.
37. **Cana (**= Santa Cruz de Cana**),** 07°47′N/77°42′W, 2000 and 3000 ft: ANSP 19724, 19725; USNM 178655, 179599, 179601–179603, USNM 179606. **Escucho Ruido:** ANSP 19711, 19712. **Río Escucho Ruido**: ANSP 19704, 19705.
38. **Near Río Setagentí**, 07°46′N/77°40′W, 1800 ft m: USNM 318172–318176.
39. **Cituro** (see Anthony, 1916), 08°00′N/77°36′W: AMNH 38168.
40. **Paya Village,** 07°53′N/77°24′W: USNM 310567, 310570, 314581. **Boca de Río Paya:** USNM 306962.
41. **Tapalisa** (see Anthony, 1916), 07°59′N/77°26′W, 1000 ft: AMNH 37916–37922, 37928, 37929.
42. **Casita (**= Tacarcuna Casita**),** 08°01′N/77°22′W, 1500–1700 ft: USNM 310553–310556, 310581.
43. **Tacarcuna Village**, ‘‘former site of the Tacarcuna Yellow Fever Station, is located in the foothills of the massif of Cerros Tacarcuna and Malí . . .’’ (Voss and Emmons, 1996: 53), 08°05′N/77°17′W, 1950 and 3200 ft: USNM 244460, 310497, 310503, 310504, 310557–310565, 310575–310580, 310582–310584, 339057. **Tacarcuna** (see Anthony, 1916), 2650 ft: AMNH 37915.

COLOMBIA

Departamento del Chocó

44. **Unguía,** which is ‘‘in lowlands close to Golfo de Urabá 15 km W of Río Atrato and 19 km SE of Cerro Tacarcuna on Panama border’’ (Paynter and Traylor, 1981: 266), 08°01′N/77°04′W, sea level: FMNH 70498–70503, 70505, 70506, 70533, 72405, 72408.
45. **Gorgas Memorial Laboratory, Río Truandó, Teresita,** 07°26′N/77°07′W: FMNH B-643, B-928, B-932.
46. **Serranía de Baudó,** which is a ‘‘coastal range extending from Panama border S to central Chocó, separated from Western Andes by valleys of Río Atrato and Río San Juan’’ (Paynter and Traylor, 1981: 19), 06°00′N/77°05′W, 3500 ft (specimens were collected by Kerr but exact site is unknown): AMNH 33187, 33188.

Departamento de Antioquia

47. **Urabá, Río Curufao,** 08°01′N/76°44′W, 50 m: FMNH 70504.
48. **Villa Arteaga,** ‘‘western foothills of Serranía de Abibe, a northern extension of Western Andes’’ (Paynter and Traylor, 1981: 272), 07°20′N/76°26′W, 130 m: FMNH 70494–70497, 70546.
49. **Purí,** which is ‘‘at western base of northern Central Andes at confluence of Quebrada Purí and Río Cauca 20 km S of Cáceres’’ (Paynter and Traylor, 1981: 206), 07°25′N/75°20′W, 200–240 m: FMNH 70522–70526.
50. **24–26 km S and 21–22 km W Zaragoza (La Tirana),** 07°30′N/74°52′W, 540–670 m: USNM 499560–499573, 499953–499955, 500000.
51. **San Jerónimo, 35 km NW Medellín,** 06°15′N/75°35′W: FMNH 70488–70592.

Departamento de Córdoba

52. **Socorré,** ‘‘on upper Río Sinu, ca. 2.5 km below mouth of Río Verde’’ (Paynter and Traylor, 1981: 246), 07°51′N/76°17′W, 100–150 m: FMNH 69207–69213.

Departamento de Bolívar

53. **San Juan Nepomuceno,** ‘‘northern Bolívar at northeastern base of Montañas de María and Serranía de San Jacinto, 26 km N of El Carmen de Bolívar’’ (Paynter and Traylor, 1981: 229), 09°57′N/75°05′W, 167 m: FMNH 69201, 69203–69206.

Departamento del Magdalena

54. **Bonda,** ‘‘a small village on the Río Manzanares, between 8 and 9 miles east of Santa Marta, in the Sierra Nevada de Santa Marta region’’ (Hershkovitz, 1947: 40; also see Smith, 1904: 413), 11°14′N/74°13′W: BMNH 0.5.6.9 (labeled ‘‘Santa Marta’’ but collected somewhere ‘‘along the river valley

and on the mountain slopes to the southeast up to 6,000 feet or more,'' Hershkovitz, 1947: 40; also see Paynter and Traylor, 1981: 25). **Río Manzanares,** 3000 ft: AMNH 15496, 23279.

55. **Minca,** which is ''on the western slope of the Sierra Nevada de Santa Marta about 14 miles from Santa Marta on the road to Cincinnati at the point where it crosses the Río Gaira'' (Hershkovitz, 1947: 42; also see Paynter and Traylor, 1981: 160, and Smith, 1904: 414), 11°12′N/74°04′W, 600 m: AMNH 15318 (holotype of *Oryzomys magdalenae*), 15319.
56. **Cincinati (Valparaíso),** a ''large coffee plantation, in tropical and subtropical zones on southern slope of Cerro Quemado at western end of Cuchilla San Lorenzo, formerly known as Valparaíso'' (Paynter and Traylor, 1981: 55; also see Hershkovitz, 1947: 40, and Smith, 1904: 414), 11°06′N/74°06′W, 4500 ft: AMNH 15323 (holotype of *Oryzomys mollipilosus*), 15320, 15321 (holotype of *Oryzomys villosus*), 15322, 15324–15327, 23626.
57. **Don Diego,** in ''coastal lowlands N of Sierra Nevada de Santa Marta and 55 km E of Santa Marta'' (Paynter and Traylor, 1981: 70; also see Hershkovitz, 1947: 41, and Smith, 1904: 414), 11°15′N/73°42′W, sea level: AMNH 23284, 23285, 23287–23289; CM 3113, 3118–3120, 3129, 3130, 3132–3138, 3142, 3143, 3149–3151.
58. **Palomino** (also spelled Palomina), which ''is an Indian village on the northern slope of the Sierra Nevada de Santa Marta . . . on the right bank of the Río Palomino, northwest of Pueblo Viejo and about 15 kilometers up from the mouth of the river'' (Hershkovitz, 1947: 43; also see Paynter and Traylor, 1981: 184), 11°02′N/73°39′W, 600 m: AMNH 38941.

Departamento del Cesar

59. **Colonia Agrícola de Caracolicito,** ''an agricultural colony established by the Colombian government in the valley of the middle Río Ariguaní on the southern slope of the Sierra Nevada de Santa Marta'' (Hershkovitz, 1947: 41), 10°19′N/73°51′W (from USBGN Colombia, 1988: 164; Hershkovitz [1947: 41] gave 10°18′N/74°00′W, and Paynter and Traylor [1981] recorded 10°12′N/73°58′W), 335 m: USNM 280522, 280597–280604, 280607–280616, 280619, 280620.
60. **Pueblo Viejo,** which is a ''hamlet replacing the extinct village of San Antonio on the northern slopes of the Sierra Nevada [de Santa Marta]. The village is on the Río San Antonio above its junction with the Río Macotama, whence it continues to the sea as the Río San Miguel. It lies among grass-covered hills between the tropical and subtropical zones. Several trails lead out of Pueblo Viejo, one of them west to the Indian village of Palomino'' (Hershkovitz, 1947: 43), 10°59′N/73°26′W, 853 m (8000 ft is given on tags, but Hershkovitz claims this to be an exaggeration): AMNH 38936–38940: BMNH 9.4.15.5; CM 3179; FMNH 34018; MCZ 8083–8085, 8088, 8103, 8104; USNM 85536.
61. **Pueblo Bello**, ''a village on a savanna mesa between the upper Río Ariguaní and its tributary, the Ariguanicito, on the southern slope of the Sierra Nevada de Santa Marta'' (Hershkovitz, 1947: 43); USBGN Colombia (1988) lists the place as an airfield with coordinates of 10°22′N/73°38′W, 1067 m: USNM 280623–280625.
62. **El Salado,** ''on the mule trail about halfway between Pueblo Bello and Valencia, on the eastern slope of the Sierra Nevada de Santa Marta. The site is in the center of a broad belt of forest and *rastrajo* which separates the savannas of the Río Cesar Valley from those of Pueblo Bello'' (Hershkovitz, 1947: 41), 10°22′N/73°29′W, 430 m: USNM 280626, 283080–283082.
63. **San Alberto** (see Paynter and Traylor, 1981: 221), 07°48′S/73°24′W (USBGN Colombia, 1988), 350 m: LACM 19922, 19923.

Departamento de La Guajira

64. **Villanueva,** which is a ''town at the base of the Sierra Negra (Cordillera Oriental) in the upper Río Cesar valley. The region is semiarid with a scattering of low scrubby vegetation. There still remain, however, a few isolated stands of deciduous forest which once were continuous with the forests of the Magdalena'' (Hershkovitz, 1947: 45), 10°37′N/72°59′W (USBGN Colombia, 1988), 274 m: USNM 283084, 283085.
65. **Sierra Negra,** the ''so-called 'Black Mountains' or western range of the Sierra de Perijá overlooking the town of Villanueva in the semiarid Cesar Valley'' (Hershkovitz, 1947: 44; also see Paynter and Traylor, 1981: 171), 10°37′N/72°54′W, 1265 m: USNM 283083 (the specimen came from Hershkovitz's collecting station, Pajalito, ''situated almost due east above Villanueva at an altitude of 1,265 meters,'' Hershkovitz, 1947: 44).
66. **Marimonda (**= Las Marimondas**),** ''at northwestern end of Serranía de Perijá, ca.

20 km SE of Fonseca'' (Paynter and Traylor, 1981: 155), 10°52′N/72°45′W (from Hershkovitz, 1960: 564), 11°02′N/72°55′W (listed in USBGN Colombia, 1988), 1000 m: USNM 283086–283088.

Departamento de Norte de Santander

67. **Río Tarrá**, ''A tributary of the upper Río Catatumbo on the eastern slope of the Sierra de Perijá, and not to be confused with the much larger Río Tarra of the lower Catatumbo in Venezuela. The author's collecting station was in the deep, broad, humid tropical valley of the Tarra. . . . The region is almost continuously rainy except for a definite dry season from mid-December through March. It is densely covered with virgin forests and inhabited by a small population of the primitive Motilón Indians'' (Hershkovitz, 1947: 44; also see the discussion in Paynter and Traylor, 1981: 253–254), 08°36′N/73°01′W, 200 m: USNM 283090.

Departamento de Boyacá

68. **Río Cubugón, La Argentina**, on the ''eastern foothills of northern Eastern Andes on Río Cubugón'' (Paynter and Traylor, 1981: 122), 07°00′N/72°15′W, 2400 ft: FMNH 72537.
69. **Río Cobaría Fatima**, this locality is reported as being in Departamento Arauca but ''the river flows only through Boyaca'' (Paynter and Traylor, 1981: 57), 07°03′N/72°04′W, 1100 and 2300 ft: FMNH 92533–92536.
70. **Muzo,** ''on the western slope of central Eastern Andes [Cordillera Oriental, Hershkovitz, 1960: 564], in steepsided valley of Río Minero, 105 km N of Bogotá'' (Paynter and Traylor, 1981: 168), 05°32N/74°06′W, 1100 and 1300 m: FMNH 72057–72059.

Departamento de Cundinamarca

71. **Volcanes, Municipio Caparrapi,** 05°25′N/74°35′W: USNM 282115.

Departamento de Caldas

72. **Samaná,** ''on Río Honda, S of Páramo San Félix, on eastern slope of Central Andes'' (Paynter and Traylor, 1981: 220), 05°24′N/75°00′W (USBGN Colombia, 1988), 1000 m: FMNH 72063, 72076.

Departamento del Cauca

73. **Río Mechengue** (see Paynter and Traylor, 1981: 158), 02°40′N/77°12′W, 800 m: FMNH 90215.

VENEZUELA

Estado de Zulia

74. **Misión Tukuko** (at the base of the Serraniá de Perijá; the site is described by Voss, 1991: 68–70), 09°50′N/72°52′W, 200 m: USNM 448592–448611.

74a. **Novito, 19 km WSW Machiques**, on lower eastern ''slopes of Sierra de Perijá, overlooking valley of Río Negro'' (Handley, 1976: 77), 10°02′N/72°43′W, 1131 m: USNM 442132, 495368.

75. **Hacienda El Tigre, 17 km N and 55 km W Maracaibo** (from the skin label), Handley (1976: 71) indicated that Hacienda El Tigre is ''39 km NW La Paz'' and included it in his description of Cerro Azul), 10°40′N/71°37′W (Handley, 1976: 66, gave 10°51′N/72°16′W for Cerro Azul), 80 m: USNM 442134, 442135.

Estado de Yaracuy

76. **Finca El Jaguar, 21 km (by road) NW Aroa** (''The Finca is situated in the Serranía de Aroa, a range of low mountains fronting the Caribbean littoral and separated from the Cordillera de la Costa by the depression of San Felipe'' [field journal of R. S. Voss, AMNH, Mammalogy]), 10°26′N/68°54′W (for Aroa), 700 m: AMNH 257239; MNHLS 8106, 8113.

76a. **Near Minas de Aroa, 8 km N and 18 km W San Felipe** (from skin label), Handley (1976: 77) indicated that Minas de Aroa is ''19 to 30 km NW San Felipe,'' 10°25′N/68°54′W, 403 and 404 m: USNM 442108, 442109, 442129–442131, 495367.

76b. **Palmichal, 23 km N Bejuma,** 10°03′N/68°37′W (of Palmichal, from USBGN Venezuela, 1993), 1000 m: USNM 562964.

77. **19 km NW Urama,** which is a ''cattle ranch on flat to hilly plain between Salado, Yaracuy, and Aroa rivers, inland about 15 km from coast'' (Handley, 1976: 84), 10°27′N/68°19′W, 25 m: USNM 495355.

Estado de Carabobo

77a. **San Esteban,** ''in valley on northern slope of coastal range'' (Paynter, 1982: 177), 10°26′N/68°01′W, 720 m: AMNH 31550; BMNH 11.5.25.146–11.5.25.148.

Estado de Aragua

78. **Rancho Grande,** ''research station in Parque Nacional Henri Pittier (Rancho Grande) at pass of El Portachuelo, in coastal range 25 km NW of Maracay and 25 km SE of Ocumare de La Costa'' (Paynter, 1982: 170), 10°22′N/67°41′W, 910–1170 m: AMNH 183156.

Distrito Federal

79. **Near El Limón** (= Hacienda Carapiche; see Handley, 1976: 71), **3 km S and 46 km W Caracas,** (Handley, 1976: 71), 10°29′N/67°19′W, 398 m: USNM 387857.
80. **San Julián, 8 mi E La Guaira,** ''settlement near Caraballeda on Caribbean coast'' (Paynter, 1982: 181), sea level, 10°37′N/

66°50′W, sea level: USNM 105405 (holotype of *Oryzomys medius*), 143791, 143792.

81. **Macuto,** ‘‘on Caribbean coast just E of La Guaira’’ (Paynter, 1982: 122), 10°37′N/66°52′W, sea level: USNM 102735.

Estado de Miranda

82. **Parque Nacional Guatopo** (the park straddles estados Miranda and Guárico [Paynter, 1982: 81]; at the given coordinates, the locality seems to be in Estado de Miranda), 10°05′N/66°25′W: TTU 36007, 36008.

ECUADOR

Provincia de Esmeraldas

83. **3 km W Majua** (about 33 km SSE Esmeraldas), 00°42′N/79°33′W, 640 ft: USNM 513546, 513549–513552, 513554, 513555.

84. **Cuaque,** ‘‘village on coast of northern Manabí at mouth of Río Coaque, 5 km SW of Pedernales’’ (Paynter, 1993: 46), 00°01′N/80°06′W (for Cuaque), sea level: AMNH 64773–64779.

84a. **Cerro Pata de Pájaro** (basecamp; see gazetteer for *O. bolivaris*), 00°02′N/79°59′W, 700 ft: AMNH 66236, 66237. **[Hacienda] El Destino**, 300 ft: AMNH 65760–64770, 67900.

85. **Bahía de Caráquez, Río Briceño** (spelled Briseño on skin labels)**, Hacienda San Carlos** (this is where Tate worked in 1923. In his ‘‘Journal of Field Work’’ [AMNH Mammalogy Archives], Tate wrote that he left Bahía de Caráquez [00°36′S/80°25′W, see Paynter, 1993: 15] at 9:30 AM crossing the mouth of the Río Chone to ‘‘the village of San Vincente. There my kindly host had waiting for me a barouche (drawn by a very ancient mule) and a couple of cargo animals for the baggage. I drove for an hour along a fine hard sandy beach until I reached the mouth of Río Briseño. There my host . . . appeared. . . . He conducted me to the Hacienda San Carlos, twenty minutes inland. We reached the house at 12:30.’’), 00°31′S/80°27′W (for Río Briceño, USBGN Ecuador, 1987: 27), less than 200 ft: AMNH 64733, 64736, 64780–64783, 64785–64790, 66229–66232, 66239.

Provincia de Los Ríos

86. **Vinces** (see Paynter, 1993: 218), 01°32S/79°45′W: AMNH 63101, 63102. **El Recreo (near Río Nuevo),** 01°32′S/79°44′W: USNM 534357, 534360.

86a. **Abras de Mantequilla, 13 km NE Vinces**, 01°28′S/79°40′W: USNM 513558.

87. **Limón** (G.H.H. Tate collected here and recorded in his field notes that Limón is on the road from Balzapamba [01°47′S/79°13′W, in Provincia Bolívar] to Babahoyo [01°49′S/79°31′W, in Provincia Los Ríos]), 1200 ft: AMNH 66947, 66949, 66950, 66952, 66954, 66955.

Provincia del Chimborazo

88. **Ríos Chimbo-Coco,** ‘‘at junction of Ríos Coco and Chimbo, ca. 10 mi N of Puente de Chimbo’’ (Paynter and Traylor, 1977: 29), 02°06′S/78°59′W, 2400 ft; AMNH 62314, 62315, 62317. **Hacienda Chaguarpata,** ‘‘a station in the forest above Cayandeled’’ (Chapman, 1926: 706); Cayandeled (02°07′S/78°59′W) is ‘‘on western slopes, N of Bucay, 8 km E of Río Chimbo and 30 km NW of Alausí (Paynter, 1993: 34), 2300 ft: AMNH 61628–61636.

89. **Puente de Chimbo,** ‘‘settlement [and presumably a bridge, both of which seem to have disappeared] in western foothills of the Andes, near juncture of Chimborazo, Guayas, and Bolívar, on left bank of upper Río Chimbo above railroad station at General Elizalde [Bucay], Guayas’’ (Paynter, 1993: 40; see also Chapman, 1926: 706, and Voss, 1992: 41), 02°10′S/79°10′W (from Voss, 1992: 9), 1200–2400 ft: AMNH 62198–62200, 62301–62304, 62307–62309, 62311, 62312, 62318–62326, 62328, 62329, 62331, 62335–62337, 62340–62346, 62348–62355, 62357, 63103–63111, 63313.

Provincia del Cañar

90. **San Juan, 15 m W Huigra,** ‘‘presumably this is on the railroad in extreme northern Cañar, on Chimborazo border’’ (Paynter, 1993: 183), 02°14′S/79°08′W, 870 ft: BMNH 14.4.24.19–14.4.24.22.

Provincia del Guayas

91. **Bucay (**now called General Elizalde**),** ‘‘in foothills of extreme eastern Guayas, at convergence of Guayas, Cañar, Chimborazo, and Bolívar, and on railroad and Río Chimbo’’ (Paynter, 1993: 23; also see Chapman, 1926: 704), 02°10′S/79°06′W, 1000 ft: AMNH 61343–61346.

92. **Ventura, 67 km N Bucay (**= General Elizalde**),** 1400 ft: AMNH 61637–61654, 63093–63098.

93. **El Refugio (vicinity of Dos Mangas), 5 km by road NE Manglaralto along Río Manglaralto**, 01°49′S/80°42′W: USNM 534356.

94. **Cerro de Manglaralto**, ‘‘Cerro of Manglar Alto,’’ as described by Chapman (1926: 712), who noted the place was ‘‘that portion of the Sierra de Colonche east of the town of Manglar Alto,’’ 01°50′S/80°44′W (coordinates for Manglaralto; Paynter, 1993: 119), 1200 and 1500 ft: AMNH 64791–64796, 64798–64806, 64808, 64809, 64811–64816, 64818, 64819, 64821,

64824–64836, 66350, 66363–66365. **Cerros de Colonche**, called Cordillera de Colonche by Chapman (1926: 708), who described it as ‘‘a small forested coastal range which . . . attains an altitude of about 2,600 feet east of Manglar Alto’’; Paynter (1993: 48) noted the Cerros to be ‘‘a range of hills ca. 25 km inland and roughly parallel to NW coast of Guayas, with southeastern part, near Guayaquil’’; exactly where in the Cerros the following specimen was collected is unknown: BMNH 39.129.

95. **Cerro de Bajo Verde,** which is in the Cordillera de Chongón, ‘‘20 mi NW of Guayaquil’’ (Paynter, 1993: 15; also see the discussion by Chapman, 1926: 707), 02°06′S/80°09′W: AMNH 63112–63122.
96. **Chongoncito,** ‘‘adjacent to Chongón, 25 km W of Guayaquil’’ (Paynter, 1993: 43; also see the description by Chapman, 1926: 707, and Voss, 1992: 41), 02°14′S/80°05′W, 100 m: AMNH 63092.

Provincia de El Oro

97. **Pasaje,** 03°20′S/79°40′W, 200 ft: AMNH 61340–61342.
98. **Santa Rosa,** ‘‘in central El Oro on arid coastal plain, 20 km S of Machala’’ (Paynter, 1993: 194; also see Chapman, 1926: 719), 03°27′S/79°58′W, 100 ft: AMNH 61347–61351, 73613; BMNH 0.1.1.21 (holotype of *Oryzomys sylvaticus*, collected at ‘‘Santa Rosa’’). **4 km SE Santa Rosa**, 60 ft: USNM 513562–513568.
99. **Los Pozos** (We could not find this locality on any maps. In a letter to H. E. Anthony [in AMNH Department of Mammalogy archives], G.H.H. Tate, the collector, wrote that Los Pozos was less than one day’s journey southwest from Santa Rosa, which would place it in the same general area as Arenilla [at 03°33′S/80°04′W, Paynter and Traylor, 1977: 6]. Tate indicated that he left Santa Rosa at 1:30 AM, reached Arenilla about 1:00 PM, and finally made camp at Los Pozos about 4:00 PM. ‘‘I do not believe,’’ scribbled Tate, ‘‘we are more than 200 feet above sea level.’’ He later compiled a sparsely annotated list of collecting localities where he indicated Los Pozos was at about 100 ft in Provincia El Oro. Provincia Loja is written on all the skin labels, but Tate’s letter and notes clearly identified the place as being on the coastal plain in Provincia El Oro.): AMNH 67377–67394.
100. **Salvias,** ‘‘a small hacienda on the Río Armarillo, a short distance north of Portovelo’’ (Chapman, 1926: 718; also see Paynter, 1993: 179, who noted that the coordinates for Salvias in USBGN Ecuador [1987], 03°47′S/79°21′W, place it southeast of Portovelo; our plot follows Chapman’s designation), 3500 and 4000 ft: AMNH 47806, 48445.
101. **Portovelo,** about ‘‘4 km S of Zaruma, on Río Amarillo’’ (Paynter, 1993: 161; also see Chapman, 1926: 716), 03°43′S/79°39′W, 2000 ft: AMNH 48249, 48250, 48420–48424, 48444.
102. **Río Pindo,** ‘‘a camp 6 miles east of Portovelo in a narrow valley’’ (Chapman, 1926: 718; also see Paynter, 1993: 157), 1850 and 3650 ft: AMNH 48425, 48446–48450.

Provincia de Loja

103. **Near Pta. Sta. Ana, about 10 mi SE of Zaruma on Zaruma-Loja Trail** (Zaruma is ‘‘near head of broad valley penetrating W Cordillera, on Río Amarillo, a tributary of Río Puyango’’ at 03°41′S/79°37′W, [Paynter, 1993: 226]; specimens were collected near Pta. Sta. Ana at about 03°58′S/79°28′W [estimated from map in Chapman, 1926, on which Pta. Sta. Ana is shown]), 3650 ft: AMNH 47831–47849, 48413–48419, 48427–48441.
104. **La Puente,** ‘‘about an hour south of Pullango’’ [= Puyango, 03°52′S/80°08′W, Paynter, 1993: 106]’’ (Chapman, 1926: 716), 2500 ft: AMNH 61322–61327.
105. **Puyango,** ‘‘on Loja/El Oro border, on Río Puyango [= Río Túmbez; ‘Río Pullango’ is the name Tate, the collector, used on tags and in field catalogs], near where valley broadens, 18 km NNW of Alamor’’ (Paynter, 1993: 167), 03°52′S/80°05′W, 1000 ft: AMNH 61328–61333.
106. **Quebrada Cebollal**, which is a stream, ‘‘presumably a left-bank affluent of Río Puyango, on lower slopes of extreme southwestern Loja, near Buenos Aires and N of Alamor’’ (Paynter, 1993: 34; also see Chapman, 1926: 706), 03°55′S/80°03′W, 3100 ft: AMNH 61352–61354.
107. **Alamor,** ‘‘a small town lying along a ridge between the Río Túmbez and Alamor [Río Alamor]’’ (Chapman, 1926: 703), 04°02′S/80°02′W (Paynter, 1993: 2), 4500–4550 ft: AMNH 48426, 61334–61339.
108. **Olmedo-Catacocha** (03°57′S/79°40′W–m04°04′S/79°38′W, respectively): AMNH 244459.

GAZETTEER AND SPECIMENS FOR MARGINAL WESTERN LOCALITIES OF *ORYZOMYS MEGACEPHALUS*

The lowercase letter designating each locality corresponds to a lettered symbol on the map in figure 66. Only the western portion of the geographic range of *O. megacephalus* is shown, represented by specimens we studied from places closest to the distribution of *O. talamancae* in Venezuela, Colombia, and Ecuador.

VENEZUELA

Estado de Sucre

a. **Neverí Valley**, the upper valley of the Río Neverí (Chapman, 1925: 5; Paynter, 1982: 141). The river ‘‘rises in coastal range S of Cumaná in vicinity of Cerro Turumiquire and flows E/W to discharge into sea at Barcelona’’ (Paynter, 1982: 141), 10°06′N/64°38′W, 2400 ft: AMNH 69869–69878.

COLOMBIA

Departamento de Cundinamarca

b. **Guaicaramo** (also spelled Guaycaramo on skin tags), which refer to ‘‘hills . . . at eastern base of Eastern Andes, where boundaries of Boyacá, Cundinamarca, and Meta [and Casanare] meet’’ (Paynter and Traylor, 1981: 96), 04°43′N/73°02′W: AMNH 71296–71300, 71312–71327, 71338, 76720; USNM 251961, 251964–251966.

c. **Mámbita,** ‘‘in steep-sided valley of middle Río Guavio on lower eastern slope of Eastern Andes, 85 km NNE of Villavicencio and same distance ENE of Bogotá’’ (Paynter and Traylor, 1981: 153), 04°46′N/73°19′W, 1000 m: AMNH 62245, 70526, 71301–71308, 71330–71334.

d. **Medina**, at ‘‘eastern base of central Eastern Andes, in llanos 54 km NE of Villavicencio’’ (Paynter and Traylor, 1981: 158), 04°30′N/73°21′W, 576 m: AMNH 71309, 71310, 71329, 71337.

e. **Río Guatiquía** (also spelled Guatequia on skin labels), which is a ‘‘tributary of Río Meta, originating in Eastern Andes and entering llanos near Villavicencio’’ (Paynter and Traylor, 1981: 102), 04°11′N/73°03′W: AMNH 38406, 38963.

f. **Quebrada Susumuco**, ‘‘Arises in lower eastern slope of central Eastern Andes on southern slope of Cordillera Baldío and enters left bank of Río Negro 13 km WNW of Villavicencio where altitude is ca. 800 m . . . we can find no town of Susumuco and suggest that name was used on material taken where the Bogotá/Villavicencio trail crossed the Quebrada de Susumuco at ca. 04°13′N/73°45′W’’ (Paynter and Traylor, 1981: 250): AMNH 61560, 61562; MCZ 19880–19884.

Departamento del Meta

g. **Restrepo,** ‘‘on lower eastern slope of central Eastern Andes, 15 km NE of Villavicencio (Paynter and Traylor, 1981: 212), 04°15′N/73°34′W, 600 m: AMNH 142137, 142175, 142176, 202648.

h. **Villavicencio**, at ‘‘eastern base of central Eastern Andes and on western edge of llanos, on Río Guatiquía’’ (Paynter and Traylor, 1981: 274), 04°09′N/73°37′W, 500 m: AMNH 71342, 71343, 136347, 136348, 136352, 136356, 136358, 136360, 136361, 136364, 202644, 202646; MCZ 27591.

i. **Parque Nacional La Macarena, 5 km W Duda Cabaña**, Duda Cabaña is at the ‘‘western base at middle of Serranía de la Macarena, on Río Duda, near its confluence with Río Guayabero’’ (Paynter and Traylor, 1981: 71), 02°33′N/74°02′W, 200 m: FMNH 58777.

Intendencia del Caquetá

j. **Florencia**, at ‘‘eastern base of southern Eastern Andes at junction of Río Hacha with Río Orteguaza’’ (Paynter and Traylor, 1981: 87), 01°38′N/75°36′W, 600, 675 ft: AMNH 33757–33759, 33772, 33774–33776.

k. **Tres Troncos** (see gazetteer for *O. yunganus*), 00°08′N/74°41′W, 150 m: FMNH 72035, 72048–72050, 72064, 72065.

Intendencia del Putumayo

l. **Río Mecaya, at the Río Caquetá** (see Paynter and Traylor, 1981: 157), 00°28′N/75°20′W, 185 m: FMNH 72037–72040, 72043–72047, 72052–72056, 72068–72072, 72091.

ECUADOR

Provincia de Napo

m. **Limóncocha,** ‘‘a missionary station established 1955 on unspoiled lemon-colored lake in tropical forest [now destroyed], 2 km from mouth of Río Jivino, a tributary Río Napo’’ (Paynter, 1993: 111), 00°25′S/76°38′W, 250 m: USNM 513540–513542, 528353–528355.

n. **San José Abajo** (see the gazetteer for *O. yunganus*), 00°26′S/77°20′W, 250 m: AMNH 68047, 68050, 68060, 68081, 68083–68087, 68099–68101, 68104, 68107, 68116, 68117.

o. **Ávila**, ‘‘in foothills of the Oriente, 25 km ESE of Volcán Sumaco and 25 km W of Loreto’’ (Paynter, 1993: 12), 00°38′S/77°25′W, 600 m: MCZ 38685, 52590, 52591; USNM 267501.

p. **Río Suno Abajo** (= Río Suno [Chapman, 1926: 718; Paynter, 1993: 201]), 00°42′S/77°08′W: AMNH 68051–68058, 68061–68080, 68090-68098, 68102, 68103, 68108–68114. **“Near Río Suno’’**: MCZ 27363, 27376, 27378, 27600.

q. **Concepción**, ‘‘ca. 300-500 m, 50 km NE of Tena’’ (Paynter, 1993: 50), 00°48′S/77°25′W: MCZ 52533–52539. **Río Cotapino Abajo**: MCZ 52602.

r. **Chonta-Urco** (Paynter, 1993: 44, could not locate this place and suggested it might be equivalent to ‘‘Río Chonta’’; however, he also pointed out that Hellmayr and Conover placed what they called ‘‘Chonta-Urco’’ near Archidona, 00°55′S/

77°48′W, which we accept, because ''Chonta-Urco'' is written on the skin tag and the specimen was collected by Hellmayr.): MCZ 38688.

Provincia de Pastaza

s. **Tiguino, 130 km S Coca,** 01°07′S/76°57′W, 300 m: USNM 574568.

t. **Canelos**, ''on lower slopes of the Oriente, on left bank of Río Bobonaza, 30 km SE of Puyo'' (Paynter, 1993: 29), 01°35′S/77°45′W, 530 m: AMNH 63384, 67368–67374.

u. **Sarayacu**, ''on middle Río Bobonaza, 60 km SE of Puyo'' (Paynter, 1993: 196), 01°44′S/77°29′W, 700 m: AMNH 67352, 67353, 67400.

v. **Río Jatun Yacu** (= Río Rutuno), which is ''one of the right-bank headwaters of the upper Río Bobonaza . . . northeast of Sarayacu'' (Paynter, 1993: 175), 01°55′S/77°14′W, 700 m: MCZ 37905–37916, 37954–37956.

w. **Río Tigre** (see locality 30 in gazetteer for *O. yunganus*), 02°07′S/76°04′W, 2000 ft: BMNH 54.435.

Provincia de Zamora-Chinchipe

x. **Zamora** (see locality 31 in gazetteer for *O. yunganus*), 04°04′S/78°58′W, 2000 and 3250 ft: AMNH 36566–36570, 47557, 47820–47823, 47826–47829.

DISTRIBUTION AND HABITAT

Collection localities of specimens examined indicate the range of *O. talamancae* to extend from Provincia de Guanacaste, northwestern Costa Rica, east through Panamá (''at lower elevations, probably throughout Panama,'' [Handley, 1966: 780, who treated the Panama samples as a form of *capito*]) into western Colombia, northwestern Venezuela, and the length of western Ecuador. Sea level to about 1500 m is the altitudinal bracket in which all specimens we document were collected.

Oryzomys alfaroi and *O. bolivaris,* forest-dwelling congeners of *O. talamancae,* occur with the latter in parts of its range, but their distributions also extend farther north into either Caribbean Honduras (*O. bolivaris*) or southern México (*O. alfaroi*). In contrast, we have not seen specimens of *O. talamancae* from north of the Río San Juan and southern margin of Lago de Nicaragua, which approximate the border between Costa Rica and Nicaragua, and except for the Guanacaste site (locality 1), the species has not been recorded from anywhere else within the northwestern two-thirds of Costa Rica (fig. 66).

The geographic and altitudinal distributions of *O. talamancae* and *O. bolivaris* broadly overlap (compare the maps in figs. 50 and 66), but the former ranges over a more extensive area in South America apparently reflecting its greater tolerance for drier forest habitats. *Oryzomys bolivaris,* on the other hand, seems restricted to tropical evergreen forest formations in regions characterized by high humidity and rainfall (fig. 50; table 23).

In Ecuador and southern Colombia, *O. talamancae* apparently is confined to the Pacific coastal plain and western foothills of the Andes. Its elevational range does not extend into upper montane forest, subpáramo, or páramo habitats or through passes and down into the eastern foothills. Collection records of *O. talamancae* from farther north in Colombia are scanty, but are sufficient to suggest that the species occurs in suitable habitats from low to middle elevations everywhere in western Colombia except the eastern foothills along most of the Cordillera Oriental; however, there are records near the Venezuelan border along the Río Cubugón and Río Cobaría Fatima (localities 68 and 69).

To the north and northeast in western Venezuela, we have records only from west of Lago de Maracaibo and from the western coastal range and adjacent lowlands. We have not seen specimens from eastern foothills of the Cordillera de Mérida between localities 69 in Colombia and 76 in northern Venezuela; however, Ochoa et al. (1988b) recorded *O. talamancae* from the Reserva Forestal de Ticoporo (07°49′–08°10′N/70°37′–70°55′W) in Estado de Barinas, which is in the forest between the Cordillera and the Llanos of the Orinoco. The species possibly occurs throughout that narrow forested strip that extends along the base of the Cordillera (see map of Amazonia in fig. 15 and Voss's map, 1991: 86, which help visualize the relationship of forest to Llanos along the eastern base of the Cordillera de Mérida). Longitude 66°W represents the eastern limit of the species in northern Venezuela (locality 82, Parque Nacional Guatopo) as documented by museum specimens.[6]

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[6] Pérez-Zapata et al. (1986) identified as *O. talamancae* two specimens they claimed were collected in the

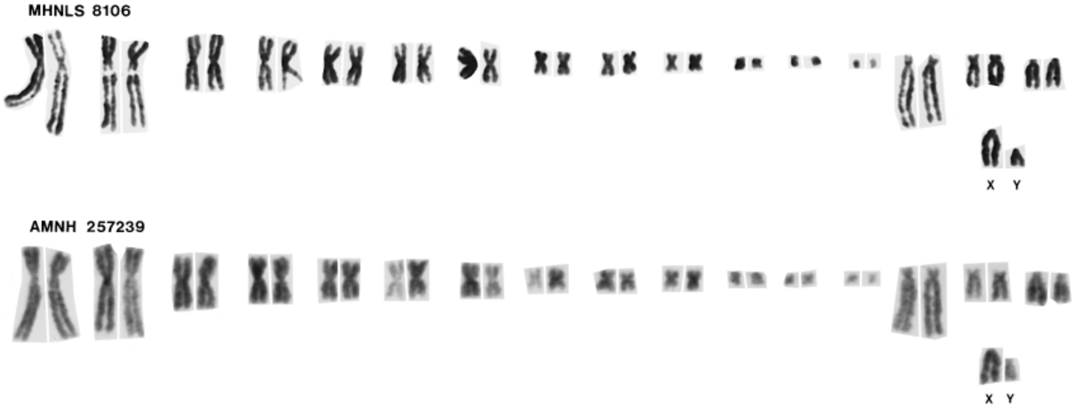

Fig. 68. Karyotypes of male *Oryzomys talamancae* ($2n = 34$, FN = 64) captured at Finca El Jaguar, 21 km (by road) NW Aroa, Estado de Yaracuy, Venezuela (locality 76 in gazetteer). Contrast these with the karyotypes in figure 69; also see discussion in text.

Alamor (locality 107) at latitude 4°S in southwestern Ecuador is the southernmost record of *O. talamancae* documented by specimens. However, we see no reasons why the species will not eventually be collected farther south in northwestern Perú.

Oryzomys talamancae inhabits tropical forests, both evergreen and deciduous. Below, we discuss examples of habitats, listed by country, gleaned from specimen labels, field journals, and publications.

Costa Rica: McPherson (1985: 221) remarked that Costa Rican collection localities for *O. talamancae* were in Holdridge’s ‘‘Tropical Moist Forest, Tropical Wet Forest, Premontane Wet Forest, and Premontane Wet Forest–Basal Transition. Data associated with a specimen from the Guanacaste region of Costa Rica [locality 1 in gazetteer] indicates it was collected in ‘primary forest, semideciduous, hilly’.’’

Panama: Handley (1966: 780) noted that specimens (identified as *O. capito*) came from ‘‘Forest, both evergreen and deciduous,’’ and Fleming (1971) studied populations (also identified as *O. capito*) in ‘‘tropical moist forest’’ on the Atlantic end of the Panamá Canal Zone and ‘‘tropical dry forest’’ on the Pacific side of the Canal Zone.

Colombia: Hershkovitz (1947) provided habitat descriptions for several localities in Colombia, many of them places he collected in or visited: **Bonda** (locality 54), ‘‘the country lies in the semiarid coastal belt and is covered, in great part, with dry forest with intervals of open grass land on the ridge’’ (p. 40)—Smith (1904: 413), one of the collectors of specimens listed in the gazetteer, described Bonda as a ‘‘Village on the river Manzanares, 7 miles east of Santa Marta. This was our headquarters during the greater part of our stay in Colombia. The village itself is only 150 feet above sea-level, but most collections were made in somewhat higher land. The country is hilly, covered in great part with dry forest with intervals of open grass land in the ridges. A thin line of mountain forest adjoins the river.’’; **Minca** (locality 55) ‘‘is in a zone between the arid scrublands of the lowlands and the humid mountain forest’’ (p. 42)—Smith (1904: 414) described Minca as a ‘‘Plantation on the river Gaira, 12 miles southeast of Santa Marta, at the lower border of the main mountain forest, which here adjoins dry forest and open grass lands;’’ **Cincinati** (locality 56) ‘‘lies between

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delta of the Río Orinoco (La Horqueta, Territorio Federal Delta Amacuro). Chromosomal and morphological traits reported for the two examples certainly support their determination. Their provenance as the Orinoco delta is most peculiar, however, considering the geographic range of *O. talamancae* we have outlined in this report. We would expect *O. megacephalus* to be found in the delta region, but not *O. talamancae*, and suspect that a misassociation of locality data with specimens, possibly in the laboratory, may be responsible for this unlikely record.

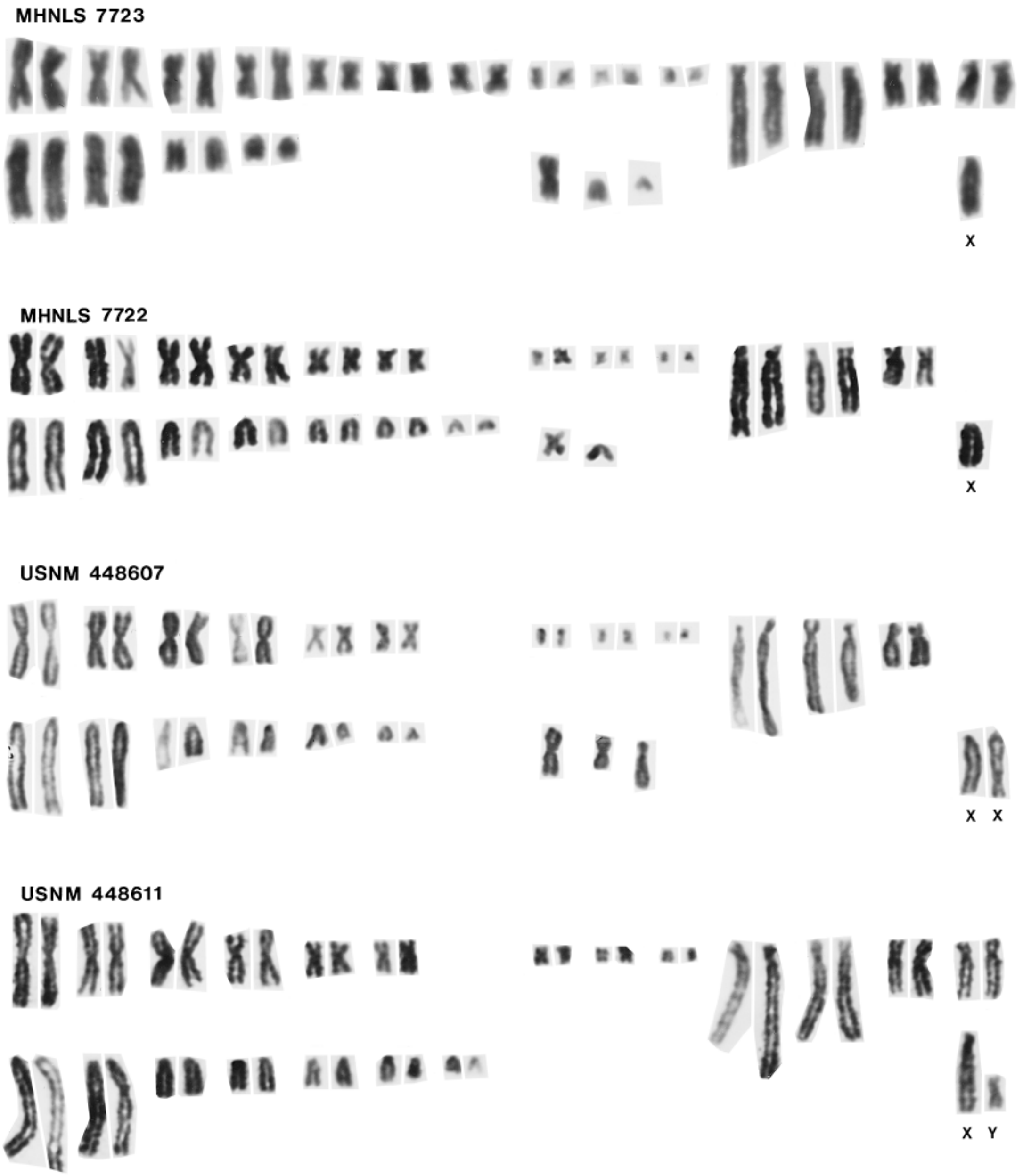

Fig. 69. Four different chromosomal patterns in the four examples karyotyped of *Oryzomys talamancae* collected at Misión Tukuko, Estado de Zulia, Venezuela (locality 74 in gazetteer). MHNLS 7723: male ($2n = 40$, FN = 66 or 67). MHNLS 7722: male ($2n = 41$, FN = 66). USNM 448607: female ($2n = 41$, FN = 66). USNM 448611: male ($2n = 42$, FN = 66). See text for elaboration.

altitudes of 900 to 1,700 meters and involves the dry tropical forests as well as the humid subtropical forests'' (p. 40); **Don Diego** (locality 57), ''The region is humid and heavily forested'' (p. 41); **Colonia Agrícola de Caracolicita** (locality 59), ''The region has been alternately cultivated and abandoned by the Indians since pre-Columbian times and most of the present forest, which is again being cut over, is not virgin'' (p. 41); **Pueblo Viejo**

TABLE 33

Records of *Oryzomys alfaroi* Captured with *Oryzomys talamancae* at Localities in Panamá, Colombia, and Ecuador[a]

(Number in parentheses at left refers to locality in gazetteer for *O. talamancae* and symbol on map in fig. 66. Specimens of *O. talamancae* from each place are listed in the gazetteer. Date indicates segment of time during which samples of both species were captured.)

Locality	*O. alfaroi*	Date
PANAMÁ		
(37) Santa Cruz de Cana	USNM 178652–178654, 178656–178659, 179912	Feb–Mar 1912
(43) Tacarcuna Village	USNM 310494–310496, 310498, 310502, 339056, 339058	Feb–Mar 1959
COLOMBIA		
(65) Sierra Negra	USNM 280560–280562	Jan 1943
(72) Samaná	USNM 72062, 72073–72075, 72077–72080	Feb 1951
ECUADOR		
(83) Majua	USNM 513547, 513548, 513553, 513556, 513557	July 1976
(87) Limón	AMNH 66948, 66951, 66953	Dec 1923
(88) Ríos Chimbo-Coco	AMNH 62313, 62316, 62338, 62339	July–Aug 1922
(89) Puente de Chimbo	AMNH 62305, 62306, 62310, 62327, 62330, 62332–62334, 62347, 62356	Aug–Sept, Nov 1922
(91) Bucay	AMNH 61343, 61344	Nov 1921
(94) Cerro de Manglaralto	AMNH 64797, 64807, 64810, 64817, 64820, 64822, 64823, 66346, 66359	May–June 1923

[a] Both species also occur in Costa Rica but we have no records of sympatry from there.

(locality 60) “lies among grass-covered hills between the tropical and subtropical zones” (p. 43); **El Salado** (locality 62) “is in the center of a broad belt of forest and *rastrajo* which separates the savannas of the Río Cesar Valley from those of Pueblo Bello” (p. 41); **Villanueva** (locality 64), “The region is semiarid with a scattering of low scrubby vegetation. There still remain, however, a few isolated stands of deciduous forest which once were continuous with the forests of the Magdalena” (p. 45); **Río Tarrá** (locality 67), “The region is almost continuously rainy except for a definite dry season from mid-December through March. It is densely covered with virgin forests” (p. 44).

VENEZUELA: Specimens collected by members of the Smithsonian Venezuelan Project are from localities described by Handley (1976), who also provided Holdridge Life Zone designations for each place: **Novito** (locality 74a), “PREMONTANE very humid forest” (p. 78); **Hacienda El Tigre** (locality 75), “TROPICAL dry forest” (p. 67); near **Minas de Aroa** (locality 76a), “PREMONTANE humid forest” (p. 77); near **Urama** (locality 77), “TROPICAL dry forest” and “TROPICAL humid forest” (p. 84); near **El Limón** (locality 79), “PREMONTANE humid forest” (p. 71).

Specimens collected by R. S. Voss and his field team in 1986 and 1987 come from two places. One series was collected near **Misión Tukuko** (locality 74) where, as Voss related in his field journal (on file at AMNH, Mammalogy), traps set in forest were

> situated near two streams a few kilometers from the Misión; the locality is known locally as Toma de Agua. Most of the traps were placed on forested hillsides covered with very tall, buttressed trees that form a closed canopy over an old cafetal [coffee plantation]; the undergrowth consists chiefly of coffee and large-leafed aroids. On some of the hillsides, considerable amounts of jagged, weathered limestone are exposed and form a labyrinth of passageways beneath the aroids, ferns and tangled debris.

Voss’s specimens of *O. talamancae* (in USNM) were collected on the ground “between buttress of tree in forest/cafetal,” on the “cafetal-forest floor,” “beside fallen log

TABLE 34
Descriptive Statistics for Selected Measurements (mm) of *Oryzomys talamancae* and *Oryzomys alfaroi* Captured at the Same Places in Ecuador (Ríos Chimbo-Coco, Puente de Chimbo, Bucay, Cerro de Manglaralto, Limón)
(Mean, ± 1 SD, and observed range in parentheses, are listed for each measurement. Samples contain both sexes and range in age from young to old adults. Specimens measured are identified in footnotes.)

	O. talamancae ($N = 38$)[a]	*O. alfaroi* ($N = 18$)[b]
LHB	121.0 ± 6.97 (109–142)	106.3 ± 5.74 (97–121)
LT	118.0 ± 8.90 (103–137)	106.2 ± 6.19 (95–117)
LHF	29.6 ± 1.40 (27–33)	27.4 ± 1.10 (25–29)
ONL	30.7 ± 1.16 (28.2–33.4)	27.4 ± 0.94 (25.9–29.8)
LB	11.9 ± 0.30 (11.3–12.7)	11.0 ± 0.24 (10.6–11.5)
LIF	4.8 ± 0.29 (4.2–5.5)	4.6 ± 0.24 (4.1–5.1)
CLM1–3	4.5 ± 0.12 (4.2–4.8)	3.9 ± 0.11 (3.8–4.2)

[a] Ríos Chimbo-Coco: AMNH 62314, 62315, 62317. Puente de Chimbo: AMNH 62199, 62301, 62303, 62307–62309, 62311, 62319, 62322, 62324, 62325, 62329, 62337, 62340, 62341, 62344, 62345, 63104, 63108, 63313. Cerro de Manglaralto: AMNH 64793, 64801–64803, 64808, 64809, 64812, 64814, 64819, 64824, 64825, 64829. Limón: AMNH 66950, 66952, 66954.

[b] Ríos Chimbo-Coco: AMNH 62313, 62316, 62338, 62339. Puente de Chimbo: AMNH 62305, 62306, 62310, 62327, 62330, 62332–62334. Bucay: AMNH 61343. Cerro de Manglaralto: AMNH 64797, 64810, 64817. Limón: AMNH 66948, 66953.

under aroids,'' ''in leaf litter in forest/cafetal,'' ''under log in forest/cafetal in dense aroid undergrowth,'' ''beneath roots of *Cecropia* in dense secondary growth in forest,'' ''on large tree trunk over dry stream bed in forest,'' and ''on tree trunk (fallen) beneath *Heliconia* in forest'' (extracted from Voss's field journal).

Finca El Jaguar (locality 76) is the other place visited by Voss and his team. Trap lines set in undisturbed forest near the finca yielded an *O. talamancae* (MHNLS 8106) that was trapped ''on ground in leaf litter among rocks and tangled undergrowth beside stream in forest'' (field journal of R. S. Voss in AMNH, Mammalogy).

ECUADOR: George H. H. Tate collected large series of *O. talamancae* from Ecuador, but his field journals (AMNH Mammalogy Archives) usually do not explicitly tie specimens to specific habitats. Exceptions are the descriptions of two of Tate's collection sites that were abstracted from his field journal by Voss (1992: 41); they are reproduced below (Voss's emendations are in brackets). Between August 3 and September 24, 1922, Tate and H. E. Wickenheiser captured 53 examples of *O. talamancae* at **Puente de Chimbo** (locality 89). Here Voss noted that ''Camped beside the Río Chimbo at 1134 ft (348 m) elevation, the collectors encountered a diversity of natural and manmade habitats:

> There are several distinct types of collecting country here.... First near the house is second-growth land and portrero [pastures]. Next, the loma [a vegetation formation peculiar to the region], forested, moderately open and dry, quite flat. Thirdly, the playas [river beaches or floodplains] and riversides, and lastly the very dense, wet montaña [forest] across the bridge from the hacienda.... From a collector's point of view this place is excellent, since besides this variety of country close by, the fauna is rich and varied. [Tate's notes for 12 August]
>
> The weather is generally true to the following program. At noon a light shower, clear p.m. and sunset; early in the evening the garúa [a dense nocturnal fog] sets in, often continuing until 8 o'clock the next morning. Morning fair till mid-day shower. In spite of this garúa, the whole second growth is arid.... The two commonest rats, *Oryzomys* [*talamancae*] and *Melanomys* [*caliginosus*] are quite generally distributed. *Sigmodon* [*peruanus*] on the other hand, I have only found in the second-growth land close to the hacienda, and in the younger part of the platanal [a garden plot] across the river, i.e., that part recently cleared, in which the logs have not decomposed. [Tate's notes for 29 August]

Here at Puente de Chimbo, Tate also recorded that members of the ''*Sylvaticus* group'' (*O. talamancae*) were ''common in second growth, the edge of forest, etc.''

Near **Chongoncito** (locality 96) at another camp, Tate collected one specimen of *Oryzomys talamancae* on October 9, 1922:

> We are actually about one half hour east of Chongoncito, encamped on an ''estero'' [a tidal estuary]. It is only salt for a short way above camp.... It gets very hot [here] through the noon hours, and is of

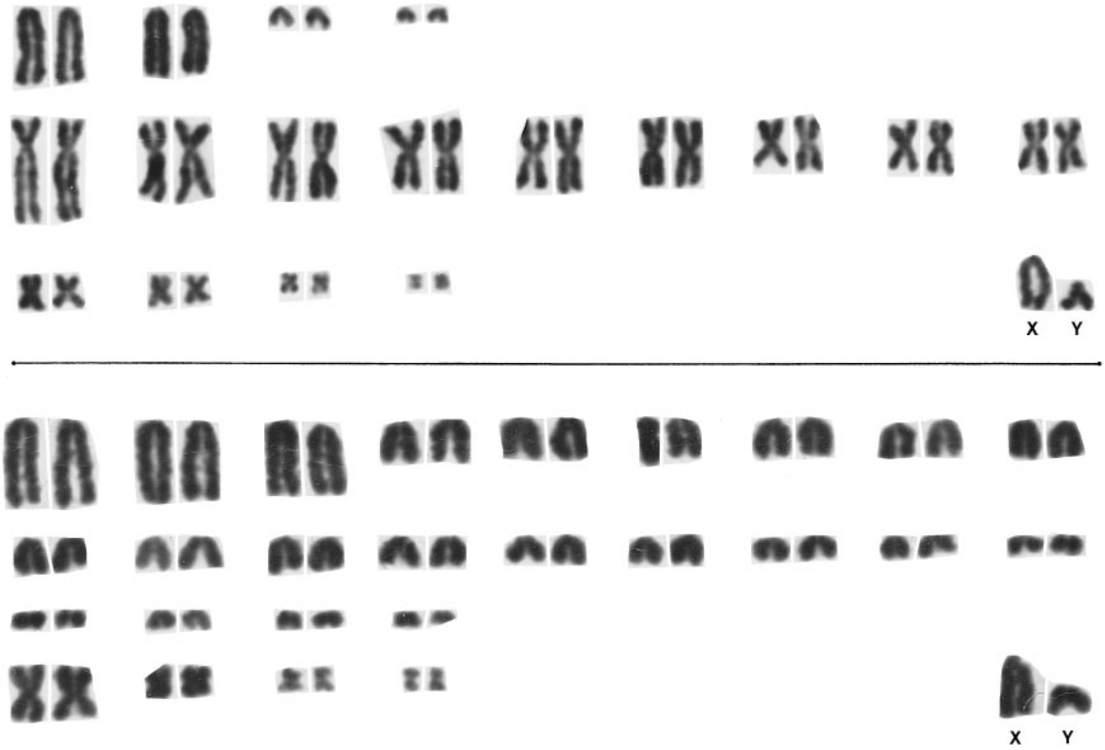

Fig. 70. Karyotypes of male *Oryzomys talamancae* from Ecuador. **Top**: USNM 513546 (2*n* = 36, FN = 60) collected 3 km W Majua (locality 83 in gazetteer), north of Golfo de Guayaquil in Provincia de Esmeraldas. **Bottom**: USNM 513567 (2*n* = 54, FN = 60) captured 4 km SE Santa Rosa (locality 98), south of Golfo de Guayaquil in Provincia de El Oro.

> course intensely dry. The country is practically flat ‘‘Ceiba country’’—thick brush interspersed with great Ceibas. [Tate’s notes for 6 October]
>
> It [the landscape] is intensely dry now, but shows evidence of being the very opposite during the rains. It is not in the least comparable with [the] Santa Elena [peninsula]. That place was purely desert, not even producing cactus. . . . One thing I fail to understand is that all this part is scrub forest averaging 15–20 feet high. Now, the people state that they take excellent crops out year after year; therefore, this smallness of the trees cannot be due to poverty of soil. The apparent reason is the long and intensely dry summer season . . . [Tate’s notes for 11 October]

In Tate’s field journals we found other information for the rodents captured that he identified as members of the ‘‘*Sylvaticus* group’’; he trapped examples of the species ‘‘mostly along the edge of woods’’ (localities l04 and l07); ‘‘arid, leafless region. About the buttress-roots of Ceiba and other large trees’’ (locality 105); ‘‘along the river where backed by woods’’ (locality 98); ‘‘humid. Taken along jungle road and in dense playa. Especially at bases of Cabouilla’’ (locality 88); ‘‘Forested, semi-arid region, trees deciduous, ground rather broken’’ (locality 99); and ‘‘under banks of dried-up streams’’ (locality 95).

Some information is associated with three localities in Ecuador at which A. L. Gardner captured *O. talamancae* (specimens in USNM). He caught the animals from near **Majua** (locality 83) on a forested (humid, mainly mature second-growth forest) ridge that extended into extensive banana groves. Traps in this forest also yielded *O. alfaroi* (USNM 513547, 513548, 513553, 513556, 513557). No examples of either species were captured in the banana grove or along a stream in brushy vegetation (here Gardner caught *Melanomys caliginosus* and *Proechimys semispinosus*) that separated adjacent banana plantings. Specimens from near **Vinces** (‘‘El Recreo,’’ locality 86) came from a patch of rather dry forest, and the series from

Fig. 71. Karyotype of male *Oryzomys alfaroi* (2*n* = 62, FN = 100) from USNM 513557 captured 3 km W Majua, Provincia de Esmeraldas, Ecuador. Compare with karyotypes of *O. talamancae* on opposite page; see also table 13 and discussion in text.

near **Santa Rosa** (locality 98) were trapped in a banana plantation. The individual from **Abras de Mantequilla** (locality 86a) was taken in the dry season and caught in a trap placed on thick leaf litter along a fence row in tall trees at the margin of a wide depression that was filled with dry leaves (which would be flooded during the wet season). The trap site was surrounded by degraded second-growth forest (2–3 years old).

CHROMOSOMES

The only published account on the chromosomes of *O. talamancae* is by Pérez-Zapata et al. (1986) who reported a diploid number of 34 and a fundamental number of 64 based on three samples from Venezuela. We found this same karyotype at another Venezuelan locality (Finca El Jaguar, Estado de Yaracuy, locality 76; table 13, fig. 68), extending the known distribution of the populations with 2*n* of 34. We found a different and variable karyotype at Misión Tukuko (Estado de Zulia, locality 74) where diploid numbers range from 40 to 42, and where we found a different chromosomal pattern in each of the four animals karyotyped (table 13, fig. 69). One male (MHNLS 7723) has a 2*n* of 40 and a FN of 66 or 67. Its chromosomal complement consists of one pair of large, three pairs of medium-sized, three pairs of small, and three pairs of very small or minute metacentrics and submetacentrics; two pairs of large and two pairs of medium-sized subtelocentrics; two pairs of large and two pairs of small acrocentrics; and four unpaired chromosomes that include one small metacentric, one small and another very small acrocentric, and the medium-sized acrocentric X chromosome, which also has very short secondary arms. The Y chromosome is one of the first three unpaired elements.

We found two different karyotypes with 2*n* of 41. One, a male (MHNLS 7722) with a FN of 66, has four pairs of medium-sized, two pairs of small, and three pairs of minute metacentric and submetacentric chromosomes; two pairs of large and one pair of medium-sized subtelocentrics; two pairs of large and a graded series of five pairs of small acrocentrics; and three unpaired ele-

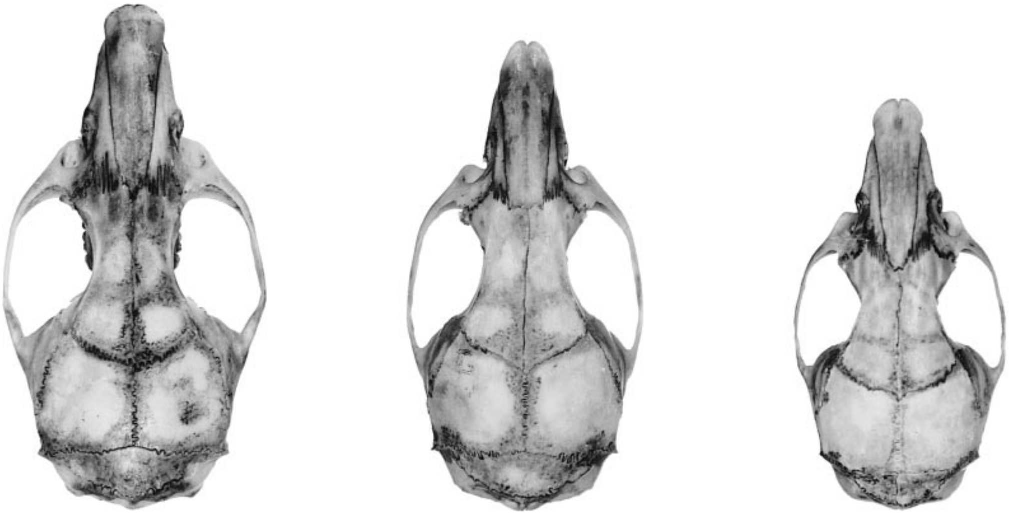

Fig. 72. Dorsal views of adult crania from Ecuadoran *Oryzomys*. On the left is *O. megacephalus* (AMNH 36577) from Zamora (locality x, figs. 66 and 67), the locality closest to the geographic range of *O. talamancae* (figs. 66, 67). Middle and right crania are *O. talamancae* (AMNH 62329) and *O. alfaroi* (AMNH 62305), respectively, both from Puente de Chimbo, Ecuador (locality 89 in *O. talamancae* gazetteer and map in fig. 66). ×2. The latter two species have also been collected together in Panamá, Colombia, and Ecuador (table 33) and are often confused with each other by collectors and researchers. Examples of *O. talamancae* are much larger than those of *O. alfaroi* (as evident here) but smaller than specimens of *O. megacephalus*; size, however, is just one of the traits that distinguishes *O. talamancae* from *O. megacephalus* (as we explain in text).

ments that include a small metacentric, a small acrocentric (one of which probably represents the Y), and the medium-sized acrocentric X chromosome, which also bears very short secondary arms.

The second karyotype with 2*n* of 41 has a FN of 66 and was found in a female (USNM 448607) whose autosomes comprise four pairs of medium-sized, two pairs of small, and three pairs of minute metacentrics and submetacentrics; two pairs of large and one pair of medium-sized subtelocentrics; two pairs of large and four pairs of small acrocentrics; and three unpaired chromosomes that include a medium-sized submetacentric, a small metacentric, and a medium-sized subtelocentric. The X chromosome is a medium-sized acrocentric with very short secondary arms.

The fourth chromosomal variant in the Misión Tukuko sample is a karyotype with 2n of 42 and a FN of 66 that was found in a male (USNM 448611). The autosomes comprise one pair of large, three pairs of medium-sized, two pairs of small, and three pairs of minute metacentrics and submetacentrics; two pairs of large and two pairs of medium-sized subtelocentrics; and two pairs of large and a graded series of five pairs of small acrocentrics. The X chromosome is a medium-sized subtelocentric and the presumed Y is a small submetacentric.

The major difference between the variable karyotypes (2*n* = 40–42) in the Misión Tukuko sample and the apparently stable karyotypes (2*n* = 34) we found in specimens from Finca El Jaguar and reported from elsewhere in Venezuela by Pérez-Zapata et al. (1986) is that the latter has an entirely biarmed autosomal complement. The number of pairs of acrocentrics in the sample from Misión Tukuko varies from four to seven, not counting the unpaired acrocentrics present in karyotypes with 2*n* of 40 and in one with the 2*n* of 41. The karyotype with 2*n* of 34 is characterized by two pairs of very large submetacentrics that are conspicuous not only for their size, but also for the secondary constrictions evident in one of the pairs. This karyotype also has

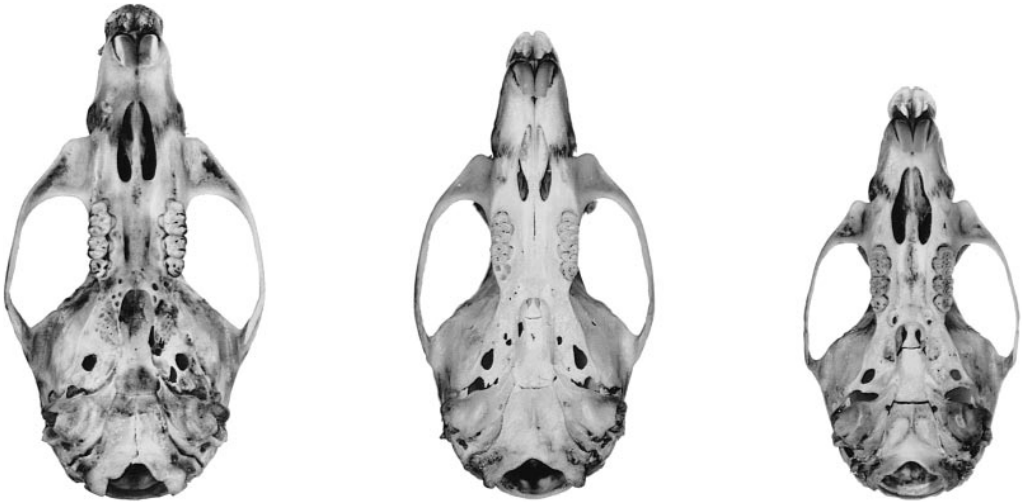

Fig. 73. Ventral views of same crania shown in figure 72. Note that in addition to absolute overall size, examples of *O. talamancae* and *O. alfaroi* also contrast in proportions of the incisive foramina (table 34). See comparisons in text.

only one pair of large subtelocentrics. In contrast, the karyotypes with 2*n* of 40–42 have an additional pair of large subtelocentrics, but lack the two pairs of very large submetacentrics. Both whole-arm translocations (Robertsonian rearrangements) and pericentric inversions are required to explain these karyotypic differences. The configurations of these karyotypes do not suggest supernumerary chromosome involvement. Random assortment within the four karyotypes we report here guarantees finding additional karyotypes in the Misión Tukuko population. We assume that Misión Tukuko is located within a zone of hybridization between populations of *O. talamancae* separated from populations characterized by the 34-chromosome karyotype. Because our assessment is based solely on the gross appearance of the chromosomes themselves, further conjecture on the nature of the variation we report here is unwarranted in the absence of additional information. Analysis of chromosomal banding patterns would help explain the nature of this variation and the relationships between this population in western Venezuela and those from elsewhere in the range of the species.

Two distinctive karyotypes characterize Ecuadoran populations, one found north and the other south of the Golfo de Guayaquil (table 13, fig. 70). Only the northern one (2*n* = 36, FN = 60, *N* = 8) shows similarity to karyotypes from Venezuelan populations. We found this karyotype in two samples (3 km W Majua, Provincia de Esmeraldas, locality 83; and Abra de Mantequilla, Provincia de Los Ríos, locality 86a). The autosomal complement consists of 1 pair of large and 1 pair of medium-sized subtelocentrics; 11 pairs of metacentrics, which can be graded into four sizes (4 large, 3 medium-sized, 2 small, and 2 minute); and 2 pairs of large and 2 pairs of minute acrocentrics. The X chromosome is a medium-sized acrocentric; and the Y is a small subtelocentric (fig. 68).

The single population sample from south of the Golfo de Guayaquil (4 km SE Santa Rosa, Provincia de El Oro, locality 98) has a 2*n* of 54 and a FN of 60 (*N* = 7). The autosomes comprise 3 pairs of large and a gradated series of 19 pairs of medium-sized to minute acrocentrics, as well as 1 pair of medium-sized, 1 pair of small, and 2 pairs of minute metacentrics. The X chromosome is a large subtelocentric; the Y, a small acrocentric (fig. 68). Although described here as a large element relative to the sizes of the other chromosomes in this complement, the X chromosomes of both Ecuadoran karyo-

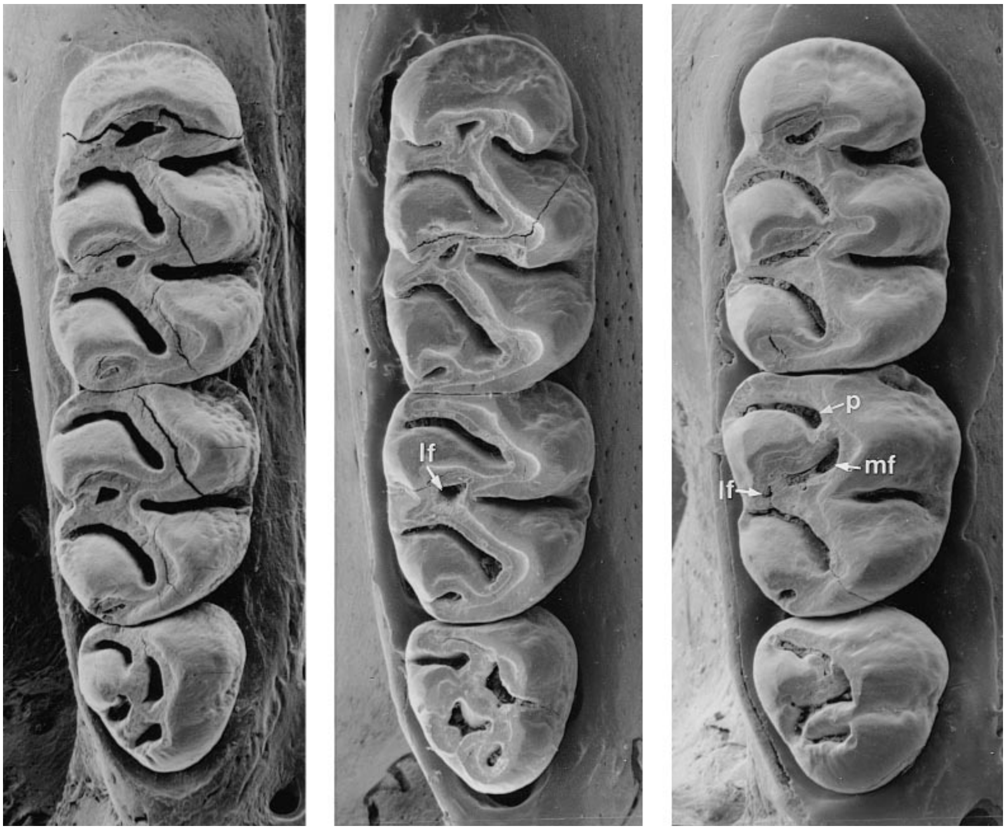

Fig. 74. Occlusal views of right upper molar rows of *Oryzomys*. **Left:** *O. megacephalus* (AMNH 231655, Perú; CLM1–3 = 5.0 mm). **Middle:** *O. talamancae* (AMNH 64806, Ecuador; CLM1–3 = 4.5 mm). **Right:** *O. alfaroi* (AMNH 64820, Ecuador; CLM1–3 = 4.1 mm). Both specimens from Ecuador were collected at Cerro de Manglaralto (locality 94 in gazetteer for *O. talamancae*), one of the sites where *O. talamancae* and *O. alfaroi* occur together (table 33). The second molars of *O. megacephalus* and *O. talamancae* have a similar coronal pattern; notice the deep paraflexus (**p**) and labial fossette (**lf**) in each. A shorter paraflexus and two fossettes—-medial (**mf**) and labial—are consistent components of the pattern in examples of *O. alfaroi*. See also figures 29 and 30.

types are of comparable size relative to the total length of all chromosomes in each karyotype.

The major differences between these two karyotypes can be explained by either fissions or whole-arm translocations (Robertsonian rearrangements). Both explanations presuppose whole-arm homologies between the chromosomes of these karyotypes, with one having been derived from the other; however, confirmation will require the analysis of banding patterns. Karyotypes from intervening populations are unknown and evidence for or against hybridization is lacking between the forms with 2*n* of 36 and 2*n* of 54.

Differences in diploid and fundamental numbers between samples from northern Venezuela and from north of the Golfo de Guayaquil seem minor. However, the variation described above for the Misión Tukuko sample from western Venezuela indicates that the similarity may be superficial and not reflective of simple geographic variation within *O. talamancae*. The contrast between samples from north and south of the Golfo de Guayaquil is impressive and suggests past isolation and differentiation of populations.

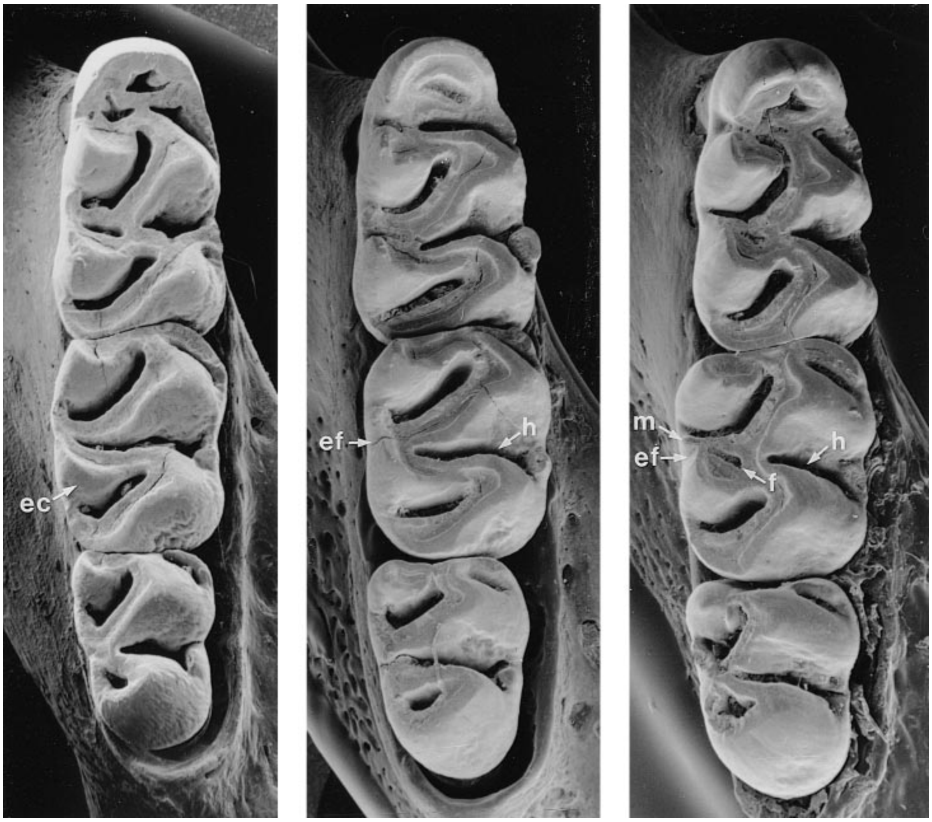

Fig. 75. Occlusal views of right lower molar rows from same specimens illustrated in figure 74. **Left:** *O. megacephalus* (clm1–3 = 5.4 mm). **Middle:** *O. talamancae* (clm1–3 = 4.7 mm). **Right:** *O. alfaroi* (clm1–3 = 4.4 mm). A deep hypoflexid (**h**), extremely shallow (essentially a vertical crease) entoflexid (**ef**), and no fossettid (**f**) characterize the second molars in examples of *O. megacephalus* and *O. talamancae*. The pattern typical of *O. alfaroi* is also common to *O. nitidus, O. macconnelli*, and *O. yunganus* (fig. 32)—a shallow hypoflexid and a fossettid formed from the entoflexid by fusion of the lingual margins of the mesolophid (**m**) and entoconid (**ec**).

We carefully examined skins and skulls from the two samples for morphological differences corresponding to the karyotypic differences, but found none. Larger samples might be more revealing; we have only eight specimens from north of the Golfo and seven from the southern locality. More extensive sampling for chromosomes in the region of the Golfo de Guayaquil also is required to determine the geographic distribution of the chromosomal forms and the presence or lack of intergradation between them.

COMPARISONS WITH OTHER SPECIES OF *ORYZOMYS*

Examples of *O. talamancae* are regularly misidentified as either *O. alfaroi* or *O. bolivaris* by collectors in the field and curators in museums. We have already contrasted *O. talamancae* with *O. bolivaris* and here we compare the former with *O. alfaroi*. We also compare samples of *O. megacephalus* with those of *O. talamancae* and contrast their geographic distributions because the latter was once considered the Central American and northwestern South American component of *O. megacephalus.*

Oryzomys talamancae and *Oryzomys alfaroi*

Musser and Carleton (1993: 720) sketched the geographic distribution of *O. alfaroi* as extending from México through Central America to western Colombia and Ecuador in lowland to lower montane forest forma-

TABLE 35

Descriptive Statistics for Cranial Measurements (mm) of Adult *Oryzomys talamancae* from Colombia and Ecuador and *Oryzomys megacephalus* from Colombia, Ecuador, and Perú

(Mean, ± 1 SD, observed range in parentheses, and number of specimens are listed for each measurement. Each sample contains specimens ranging in age from young to old adults, which are identified in the footnotes. The principal components analysis summarized in table 36 and fig. 76 is based on these specimens.)

	COLOMBIA[a]		ECUADOR and PERÚ[b]	
	talamancae (*N* = 13)	*megacephalus* (*N* = 20)	*talamancae* (*N* = 43)	*megacephalus* (*N* = 33)
ONL	31.7 ± 1.25 (29.7–34.3)	33.0 ± 1.08 (31.7–36.0)	30.9 ± 0.81 (29.0–32.2)	33.9 ± 1.16 (31.7–36.7)
ZB	15.6 ± 0.58 (14.7–16.8)	16.0 ± 0.58 (15.1–17.5)	15.4 ± 0.45 (14.5–16.2)	16.9 ± 0.82 (15.1–18.5)
IB	5.1 ± 0.19 (4.9–5.6)	5.1 ± 0.24 (4.7–5.7)	5.0 ± 0.16 (4.7–5.3)	5.3 ± 0.25 (4.9–6.1)
LR	10.1 ± 0.54 (9.3–11.2)	10.6 ± 0.46 (9.8–11.7)	9.6 ± 0.43 (8.6–10.4)	10.6 ± 0.47 (9.9–11.8)
BR	5.9 ± 0.38 (5.4–6.7)	6.2 ± 0.41 (5.5–7.4)	5.6 ± 0.23 (5.0–6.0)	6.4 ± 0.41 (5.7–7.4)
LB	12.3 ± 0.37 (11.7–13.0)	12.2 ± 0.33 (11.6–13.1)	11.9 ± 0.26 (11.4–12.6)	12.3 ± 0.55 (11.5–13.8)
HBC	8.4 ± 0.39 (7.9–9.3)	8.7 ± 0.34 (8.1–9.6)	8.5 ±0.31 (7.9–9.3)	9.1 ± 0.48 (8.0–10.2)
BZP	3.1 ± 0.31 (2.6–3.7)	3.5 ± 0.24 (3.0–4.0)	3.2 ± 0.19 (2.8–3.5)	3.8 ± 0.28 (3.3–4.3)
LD	8.3 ± 0.57 (7.5–9.5)	8.3 ± 0.38 (7.6–9.0)	7.6 ± 0.32 (7.0–8.4)	8.8 ± 0.41 (8.2–9.8)
LBP	6.8 ± 0.35 (6.2–7.3)	7.1 ± 0.29 (6.5–7.5)	6.4 ± 0.31 (5.9–7.3)	7.6 ± 0.48 (6.6–9.0)
PPL	10.9 ± 0.53 (9.9–12.1)	11.1 ± 0.47 (10.2–12.2)	10.6 ± 0.37 (9.7–11.5)	11.6 ± 0.51 (10.9–13.1)
LIF	4.4 ± 0.38 (3.6–5.1)	4.8 ± 0.31 (4.2–5.5)	4.6 ± 0.25 (4.0–5.0)	4.5 ± 0.33 (4.0–5.3)
BIF	2.5 ± 0.25 (2.2–2.9)	2.3 ± 0.16 (2.1–2.7)	2.1 ± 0.14 (1.9–2.5)	2.3 ± 0.19 (1.9–2.7)
CLM1-3	4.5 ± 0.12 (4.3–4.7)	5.1 ± 0.14 (4.8–5.3)	4.5 ± 0.16 (4.2–5.0)	5.1 ± 0.15 (4.7–5.5)
BM1	1.3 ± 0.06 (1.2–1.4)	1.5 ± 0.05 (1.4–1.6)	1.3 ± 0.06 (1.2–1.4)	1.5 ± 0.08 (1.3–1.7)

[a] *Oryzomys talamancae:* 24–26 km S and 21–22 km W Zaragoza (locality 50 in gazetteer for *O. talamancae*); USNM 499560–499571, 499573. *Oryzomys megacephalus:* Guaicaramo (locality b in gazetteer for *O. megacephalus*); AMNH 71297, 71298, 71300, 71312–71314, 71316–71319, 71321–71325, 71327, 71338, 76720; USNM 251964, 251966.

[b] *Oryzomys talmancae:* ECUADOR. Puente de Chimbo (locality 89 in gazetteer for *O. talamancae*); AMNH 62198, 62300, 62307–62309, 62311, 62313, 62319, 62322, 62328, 62329, 62337, 62340–62346, 62348, 62349, 62354. Near Pta. Sta. Ana, about 10 mi SE of Zaruma on Zaruma–Loja Trail (locality 103); AMNH 47831–47833, 47836, 47837, 47839, 47841, 47844, 47846–47848, 48413–48418, 48420, 48427, 48428, 48431. *Oryzomys megacephalus:* ECUADOR. Limóncocha (locality m in gazetteer for *Oryzomys megacephalus*); USNM 513540–513542, 528353, 528355. San José Abajo (locality n); AMNH 68048, 68060, 68084, 68086, 68087, 68101, 68104, 68107. Ávila (locality o); USNM 267501. Río Suno Abajo (locality p); AMNH 68051, 68072, 68074, 68075, 68079, 68088, 68093, 68095–68097, 68111, 68113, 68114. Sarayacu (locality u); AMNH 67352, 67400. Zamora (locality x); AMNH 36577, 47822. PERÚ. Huachi (locality 33 in gazetteer for *O. yunganus*); BMNH 54.423, 54.424.

tions. The range of this species and that of *O. talamancae* broadly overlap through Costa Rica, Panamá, and western Colombia and Ecuador. Specimens of each species have been collected at the same locality in Panamá, Colombia, and Ecuador (table 33).

In his treatise on ''The rice rats of North America,'' Goldman (1918: 60) noted how ''The general range of *alfaroi* overlaps that of *O. talamancae*, and as it may closely resemble that species in general appearance some confusion of the two has resulted.'' Color of fur is similar between adult *O. alfaroi* and young adult *O. talamancae*, and series in several museums identified as the former have proven to be examples of *O. talamancae* with fresh adult coats or in juvenile–adult transitional pelage. The dorsal and ventral fur of *O. talamancae* is brighter in most specimens, not as dark and somber as the fur of many *O. alfaroi*. The two species differ in body size, and *O. alfaroi* has longer incisive foramina relative to length of cranium (figs. 72, 73; table 34). In addition to length of molar row (table 34), occlusal surface patterns of second upper and lower molars also can be used to separate samples of *O. talamancae* and *O. alfaroi* (figs. 74, 75). All examples of *O. talamancae* we examined lack the medial fossette in the second upper molar and have a deep hypoflexid that cleaves at least three-fourths of the second lower molar—configurations like those of *O. megacephalus*. In contrast, second upper molars of *O. alfaroi* have a medial fossette, and second lower molars exhibit a short hypoflexid—patterns shared with *O. yunganus*, *O. nitidus*, and *O. macconnelli* (figs. 30, 32).

Chromosomal contrasts between the two species are striking in diploid and fundamental numbers. Sampled populations of *O. talamancae* have diploid numbers of 34, 36, 40–42, and 54, with fundamental numbers ranging from 60 to 67 (table 13; figs. 68–70). The only reported karyotype of *O. alfaroi*, which is based on a sample from México (Haiduk et al., 1979), has a $2n$ of 60 and a FN of 104. Here we report another karyotype ($2n = 62$, FN = 100; fig. 71, table 13) based on four animals from 3 km W Majua, Provincia de Esmeraldas, Ecuador (locality 83).

Oryzomys talamancae and *Oryzomys megacephalus*

From the time it was described by Allen in 1891 until 1960, the name *talamancae* identified a species that, in Goldman's (1918: 73) words, occurs in ''heavily forested regions from eastern Costa Rica eastward through Panama to near Colombian frontier; altitudinal range from sea level to 3,000 feet; Arid and Humid Lower Tropical Zones.'' Between 1960 and the early 1980s, Hershkovitz's (1960: 544) revision by footnote submerged *talamancae* into *O. laticeps*, a name replaced by *capito* (Hershkovitz, 1959, 1960) and used to designate a species ranging throughout tropical South America and into Central America (Handley, 1966: 780; Hall, 1981: 618). By 1983, Gardner (1983a: 485) had extracted *talamancae* from *O. capito* and reinstated it as a valid Costa Rican species; two years later Musser and Williams (1985) amplified its geographic and morphological definition. The specific integrity of *O. talamancae* is no longer questioned (Musser and Carleton, 1993: 725), but the distributional, morphological, and chromosomal distinctions between it and *O. megacephalus* (the name replacing *capito*) have not been adequately clarified. We now provide those contrasts here.

DISTRIBUTION: We have already outlined the geographic range of *O. megacephalus* as we understand it from specimens examined: eastern Paraguay, the Amazon Basin, Guiana Region, Trinidad, and the southern Venezuelan drainage basin of the Río Orinoco. The distribution lies to the south and east of the range of *O. talamancae*, and nowhere do the two ranges overlap. The distribution map for *O. talamancae* (fig. 66) also depicts localities for specimens of *O. megacephalus* collected along the western margin of its range where it approaches the eastern limits of *O. talamancae*. These localities were described following the gazetteer for *O. talamancae*; the documented specimens are simply those we had at hand, not all the material that is probably available in museum collections.

The Andes separate the two species in Ecuador and southern Colombia. *Oryzomys megacephalus* is found along the western rim of the Amazon Basin and penetrates the eastern foothills of the Andes, usually at elevations below 1000 m. In this region, the nearest collection records of *O. talamancae* and *O. megacephalus* are in southern Ecuador (fig. 67). There, *O. talamancae* ranges from lowlands up to about 1220 m (localities near Zaruma), but always on western slopes and valleys drained by rivers flowing to the Pacific Ocean. The nearest collection sites for *O. megacephalus,* at 610 and 990 m near Zamora, are the nearest localities for *O. megacephalus,* and are in the valley of the Río Zamora, which flows eastward into the Amazon Basin. Wet and humid montane forest formations cover higher elevations between Zaruma and Zamora, and presumably form an ecological barrier separating the two species. The geographic and vegetational relationship between *O. talamancae* and *O. megacephalus* indicated here for available samples from southern Ecuador may typify the distribution of each to the north in southern Colombia.

Farther north in Colombia, specimens of *O. megacephalus* are known from scattered sites along the eastern foothills of the Cordillera Oriental and adjacent lowlands, extending from the Serranía de la Macarena (locality i) northeast to the region between the Andean foothills and the Llanos of the Orinoco (Guaicaramo through Villavicencio, localities b–h; fig. 66). At this point the nearest collection localities for *O. talamancae* are on the western slope of the Cordillera Oriental at Volcanes (locality 71) and Muzo (locality 70).[7]

We have not seen examples of either *O. megacephalus* or *O. talamancae* from the forested strip between the Cordillera Oriental and Llanos of the Orinoco north of Guaicaramo (locality b) in Colombia. *Oryzomys talamancae* has been taken on the eastern flanks of the Cordillera Oriental along the Río Cubugón (locality 68) at 732 m and along the Río Cobraría Fátima (locality 69) at 335 and 701 m near the Venezuelan border, and the species ranges to the northeast (Ochoa et al., 1988b) into the western coastal range of Venezuela to about longitude 66°W. *Oryzomys megacephalus* apparently does not occur in this region and is found only to the east of the Llanos of the Orinoco, where the nearest records are from eastern Estado de Bolívar (Ochoa et al., 1988b) in central Venezuela and from the upper Neverí Valley (locality a) at 732 m in the eastern coastal highlands south of Cumaná. In northern Venezuela, *O. megacephalus* occurs north of the Orinoco in the eastern coastal mountains (AMNH series from Neverí and holotype of *O. modestus* from Campo Alegre at 915 m), but the western coastal highlands are inhabited by *O. talamancae.*

Based on specimens examined, we can summarize the complementary pattern of the two distributions as follows. The western

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[7] We have seen specimens of both *O. talamancae* and *O. megacephalus* that are labeled as being caught at ‘‘Muzo.’’ Three *O. talamancae* (FMNH 72057–72059) were collected by Phil Hershkovitz who wrote Musser that ‘‘My trip to Muzo was inspired by the few things Thomas described from the area and you can be sure my specimens are from there’’ (Hershkovitz, letter in AMNH Mammalogy Archives). Two *O. megacephalus* (AMNH 62783 and 62785) are represented by skins and skulls, and the only information on the skin labels is the location (Muzo), a date (September 1919), and the notation ‘‘N. Maria.’’ These two were among the lots of specimens sent by Hno. Nicéforo M. to H. E. Anthony and G.H.H. Tate at the American Museum of Natural History for their identifications. The labels attached to the specimens are American Museum tags and the data were undoubtedly recorded on them after the specimens were received in New York. Unfortunately, we cannot verify that Muzo is the collection site of these specimens and suspect they were mislabeled. *Oryzomys talamancae* occurring in Muzo is consistent with the geographic range of that species as we understand it from available samples (fig. 66); the record of *O. megacephalus* from there does not make sense considering its known geographic distribution. Muzo is separated from the nearest collection localities for *O. megacephalus* (b–h, fig. 66) in the eastern foothills and adjacent lowlands of the Cordillera by high-altitude formations of wet montane forest and patches of páramo (Espinal and Montenegro, 1963), zones from which both *O. megacephalus* and *O. talamancae* are ecologically excluded. *Oryzomys talamancae* ranges throughout northern Colombia and western Venezuela, extends into the eastern foothills of the Cordillera Oriental near the Colombia–Venezuela border (localities 68 and 69, fig. 66), and has been collected in the lowlands adjacent to the eastern foothills of the Cordillera de Mérida (Ochoa et al., 1988b); the distribution of *O. megacephalus*, however, is to the east of the Cordillera Oriental in Colombia and the Llanos of the Orinoco in central and northern Venezuela.

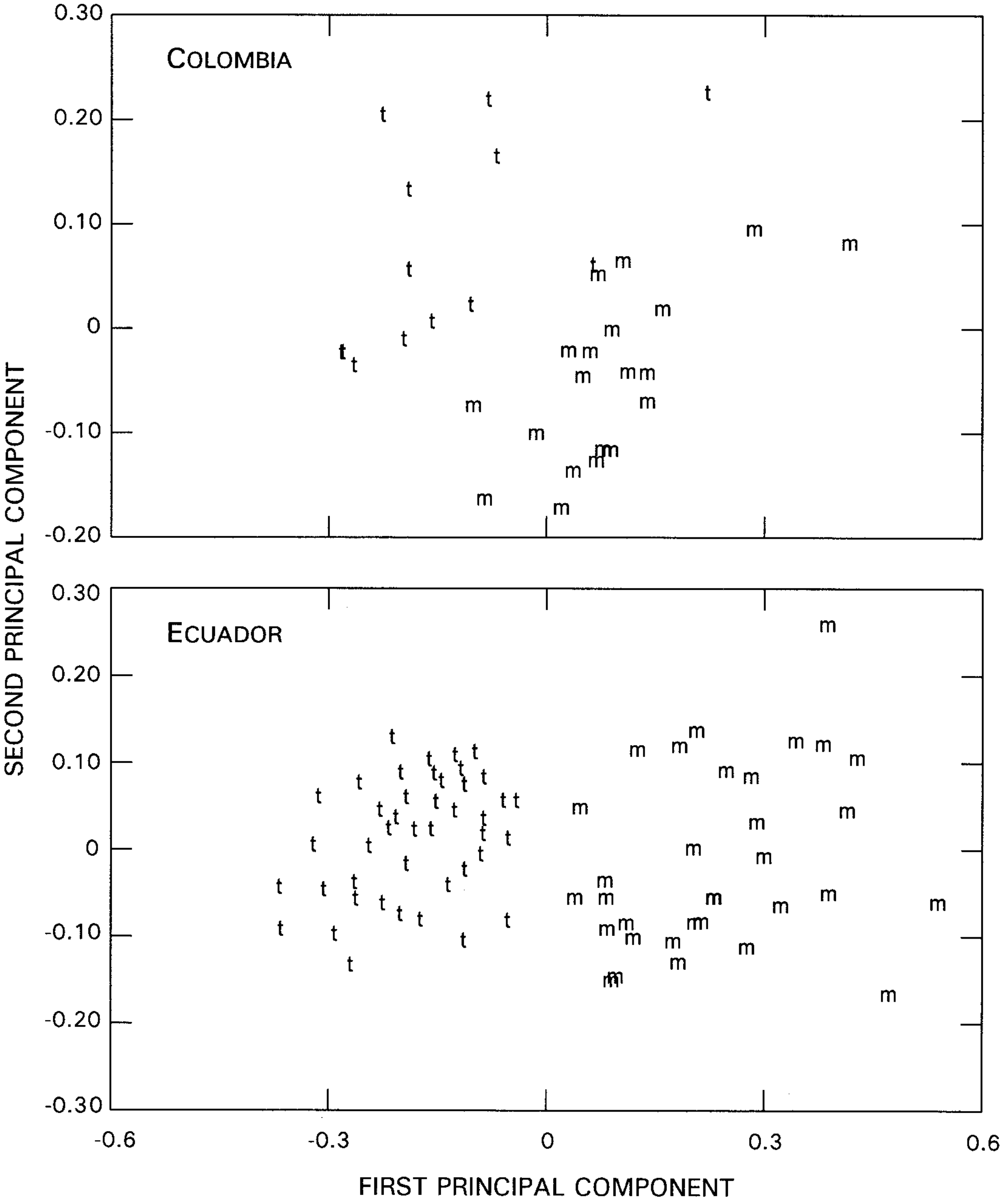

Fig. 76. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 36) and projected onto the first and second principal components extracted from analysis of young to old adult *O. talamancae* (**t**) and *O. megacephalus* (**m**). **Top**: *O. talamancae* (*N* = 13) and *O. megacephalus* (*N* = 20) from Colombia. **Bottom**: *O. talamancae* (*N* = 43) from Ecuador and *O. megacephalus* (*N* = 33) from Ecuador and one locality in Perú. See discussion in text and summary statistics in table 35.

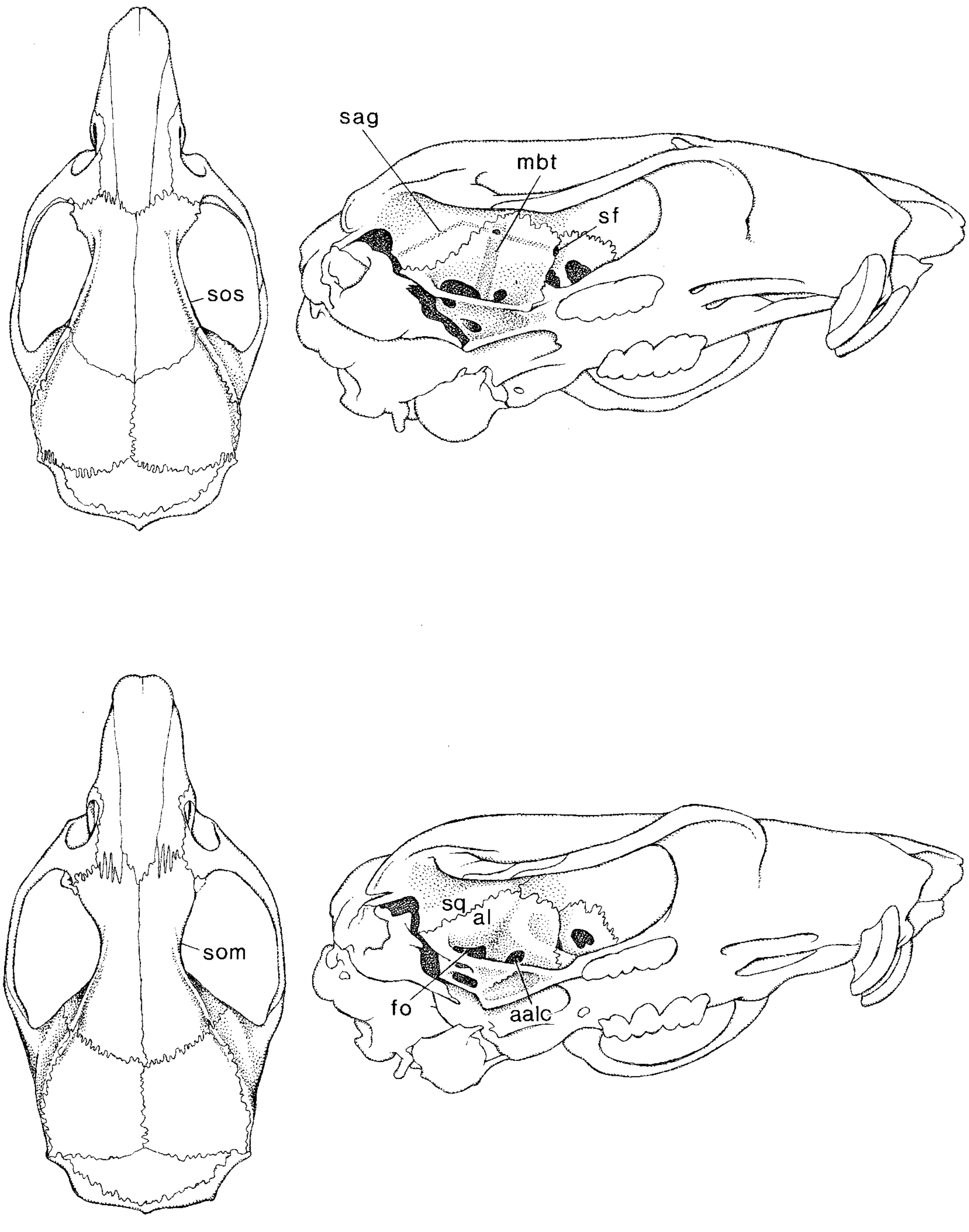

Fig. 77. Two sets of qualitatively contrasting morphologies between adult *Oryzomys* from Ecuador. **Top:** *O. talamancae* (AMNH 47839; captured 10 mi SE Zaruma, locality 103 in figures 66 and 67). **Bottom:** *O. megacephalus* (AMNH 36577; from Zamora, locality x in figs. 66 and 67). **Left** (dorsal views of cranium): Dorsolateral interorbital margins of *O. talamancae* are defined by prominent supraorbital ridgelike shelves (**sos**), but consist of smooth margins in *O. megacephalus* (**som**). **Right** (lateral views highlighting squamosoalisphenoid region): A squamosoalisphenoid groove (**sag**), in which the supraorbital branch of the stapedial artery courses, and a sphenofrontal foramen (**sf**), through which the

range of *O. megacephalus* in Ecuador and Colombia is bounded by eastern foothills of the Andes and Cordillera Oriental. In most of northern Venezuela, the Llanos of the Orinoco lie between the ranges of *O. talamancae* in the west and *O. megacephalus* in the east. Toward the Venezuelan coast, the Llanos merges with the southern limits of the "Eastern Caribbean Dry Zone," where, in Voss's (1991: 88) description, "Thornscrub and other kinds of dry vegetation are . . . encountered in the Río Unare drainage and along the eastern Caribbean coast, including the Araya Peninsula and some littoral areas of the Paria Peninsula." *Oryzomys talamancae* occurs in the northern coastal mountains to the west of this unforested coastal region; *O. megacephalus* is found in the coastal highlands to the east of the dry zone.

Range overlap of *O. talamancae* and *O. megacephalus* cannot be documented by specimens available to us. The most plausible area to expect sympatry or close parapatric association is in the forested zone along the eastern base of the Cordillera Oriental between Guaicaramo (locality b, fig. 66) in the south, where *O. megacephalus* has been recorded, and the Colombia–Venezuela border to the northeast (localities 68 and 69, fig. 66), where we have documented *O. talamancae*.

MORPHOLOGY: Examples of *O. talamancae* differ from those of *O. megacephalus* in external and cranial features, but not in molar occlusal patterns (figs. 74, 75). Bright and tawny dorsal fur, which is reminiscent of *O. nitidus*, characterizes most specimens of *O. talamancae*; pelage of *O. megacephalus* is darker, the tones flat and muted. *Oryzomys talamancae* has a distinctly bicolored tail for about three-fourths of its length; in *O. megacephalus*, tails range in pigmentation from monocolor and dark brown to slightly paler or mottled on the ventral surface.

TABLE 36

Results of Principal Components Analyses of Adult *Oryzomys talamancae* from Colombia and *Oryzomys megacephalus* from Colombia, Ecuador, and Perú

(Component loadings most strongly influencing dispersion of scores are in boldface. Actual values are summarized statistically in table 35 and were obtained from the specimens listed in that table. See fig. 76.)

	Principal components			
	COLOMBIA and PERÚ		ECUADOR	
Variable	First	Second	First	Second
ONL	0.036	0.006	**0.057**	−0.008
ZB	0.030	0.005	**0.052**	0.006
IB	0.016	0.006	0.029	0.009
LR	**0.040**	0.005	**0.058**	0.012
BR	**0.054**	0.021	**0.078**	0.006
LB	0.010	0.010	0.027	0.002
HBC	0.028	0.002	**0.041**	−0.008
BZP	**0.083**	−0.010	**0.101**	0.005
LD	0.035	0.030	**0.082**	−0.002
LBP	0.032	0.006	**0.091**	**−0.037**
PPL	0.033	0.017	**0.049**	−0.004
LIF	**0.072**	0.010	0.002	**0.055**
BIF	0.004	**0.077**	**0.040**	**0.050**
CLM1-3	**0.043**	**−0.038**	**0.058**	−0.004
BM1	**0.053**	**−0.043**	**0.059**	0.007
Eigenvalue	0.028	0.011	0.055	0.007
% Variance	49.2	20.0	66.6	9.0

Variation in cranial and toothrow dimensions distinguishes the two species. Specimens of *O. talamancae* have, on average, smaller crania and shorter molar rows than do examples of *O. megacephalus* (table 35). Results of principal components analyses reflect this division (fig. 76). The disjunction of scores for Ecuadoran and Peruvian specimens into discrete clusters along the first principal component is influenced by variation in most cranial and all dental measurements (table 36), reflecting overall size. Vari-

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artery exits into the orbit, signal the primitive cephalic arterial pattern characteristic of *O. talamancae* (similar to that in *Microryzomys*; see fig. 21 in Carleton and Musser, 1989: 39). The corresponding artery, groove, and foramen are absent in *O. megacephalus*, which possesses a derived cephalic arterial pattern similar to that in *Oligoryzomys* (diagramed in Carleton and Musser, 1989: 39). Other abbreviations: **aalc**, anterior opening of alisphenoid canal; **al**, alisphenoid; **fo**, foramen ovale; **mbt**, trough for masticatory–buccinator nerve; **sq**, squamosal.

ation in breadth of zygomatic plate is especially noticeable; *O. megacephalus* has a much wider plate than does *O. talamancae*. There is slight overlap in scores for Colombian specimens, and the dispersion is affected primarily by variation in length and breadth of rostrum, particularly breadth of zygomatic plate, length of incisive foramina, length of molar row, and breadth of first upper molar (all greater in *O. megacephalus*; table 35).

Two qualitative cranial traits consistently distinguish specimens (fig. 77). *Oryzomys talamancae* has low but definite supraorbital ridges outlining the interorbit and sweeping back along dorsolateral margins of the braincase in the form of temporal ridges. Comparable expression of ridging is not characteristic of *O. megacephalus*; slight beading along the postorbital and temporal margins represents the maximum expression we have noticed.

All specimens of *O. talamancae* studied have a sphenofrontal foramen and squamosoalisphenoid groove on the inside wall of the braincase (fig. 77). These landmarks point to a primitive carotid circulatory pattern (see Musser and Williams, 1985), a trait that is also shared by *O. bolivaris, O. nitidus, O. macconnelli, O. alfaroi,* and other species (fig. 151, table 52). Examples of *O. megacephalus* have neither a sphenofrontal foramen nor a squamosoalisphenoid groove, an indication that the supraorbital branch of the stapedial artery is absent. This pattern is common to both *O. megacephalus* and *O. yunganus* (fig. 151, table 52).

CHROMOSOMES: Except for specimens of *O. talamancae* ($2n = 54$, FN = 60) from south of the Golfo de Guayaquil, Ecuador, samples of the species in Venezuela and Ecuador have diploid numbers of 34, 36, and 40–46, with a range of fundamental numbers from 60 to 67 (table 13, figs. 68–70). Diploid numbers are either 52 or 54 among samples of *O. megacephalus* from Perú, Brazil, Venezuela, and Surinam. Fundamental numbers are 58 and 59 in the Surinam series, but 62 for all other samples (table 13). The Santa Rosa (locality 98) karyotype of *O. talamancae* is superficially similar to the karyotype ($2n = 54$) of *O. megacephalus* (compare figs. 11 and 70). Although the differences between the karyotypes of each species seem lesser in magnitude than that now known for the range of variation in *O. talamancae*, this similarity should not be interpreted as indicating any particularly close relationship.

SUMMARY

Oryzomys bolivaris can be recognized by a suite of distinctive morphological traits. Its geographic range in the trans-Andean region is closely tied to ever-wet and humid tropical evergreen forests extending from coastal lowlands to midmontane elevations and is concordant with the distributions of other rodents tied to the same forest environments.

Morphology and body size of *O. bolivaris* are similar to *O. talamancae*, another trans-Andean species. However, *O. talamancae* has a broader geographic range that embraces a wider range of forest formations and associated rainfall and humidity regimes from pluvial evergreen to dry deciduous forests. *Oryzomys talamancae* and *O. bolivaris* have been collected together at several sites; unfortunately, no studies have been undertaken at these locations to determine the ecological interactions between the species.

Segments of the geographic ranges of *O. bolivaris* and *O. alfaroi* also overlap, and examples of co-occurrence are documented from localities in Costa Rica and Ecuador. Young of each species are often mistaken as one or the other by collectors and museum workers; however, a suite of external, morphometric, and molar occlusal patterns distinguishes the two species.

Oryzomys talamancae occurs in forest and is trans-Andean in geographic distribution, with its range extending from Costa Rica through Panamá, south into the western lowlands and foothills of the Andes in Colombia and Ecuador, and eastward into northern Colombia and western Venezuela. Documented collection records indicate the known distribution of *O. talamancae* to be allopatric to that of the Amazonian *O. megacephalus*, but sympatric with both *O. bolivaris*, another trans-Andean oryzomyine, and *O. alfaroi*, which ranges from southern México through Central America to the lowlands and adjacent Andean flanks of Colombia and Ecuador. Although once considered to be the same species as *O. megacephalus*, and often misidentified as either *O. bolivaris* or *O. alfaroi*, discrete qualitative traits and morphometric features unambiguously distinguish all examples of *O. talamancae* from all samples of those three species.

THE *ORYZOMYS NITIDUS* GROUP—*O. NITIDUS*, *O. MACCONNELLI*, A NEW SPECIES FROM BRAZIL, AND *O. RUSSATUS*

In *Mammal Species of the World*, Musser and Carleton (1993: 723) provided this summary about the close morphological similarity among taxa associated with *O. nitidus* as well as the direction of future inquiry: ‘‘*Oryzomys intermedius*, *O. legatus*, *O. macconnelli*, and *O. nitidus* form a closely-related complex whose interrelationships, specific stature, and distributions deserve investigation.’’ They also listed *O. kelloggi* and *O. lamia* as species, noting that their identities, with respect to *O. intermedius*, required clarification.

This section documents results of our investigation into the identities of those six taxa. We discovered that the names can be allocated to four species: *O. nitidus*, *O. macconnelli*, an undescribed species occurring in the central part of Estado de Pará, Brazil (the Pará Sample in the gazetteer), and *O. russatus*, which is an older available name for *intermedius*. We will demonstrate that *kelloggi* simply identifies another Brazilian sample of *O. russatus*, that *lamia* represents a large-bodied geographic segment of *O. russatus* in south-central Brazil, and that *legatus* is the morphological counterpart of *O. russatus* in southern Bolivia and northern Argentina.

Our conclusions are based on study of 921 specimens of the *nitidus* group. These examples, as well as the localities at which they were collected, are listed in the gazetteer that follows. From this total number, we assembled 502 cranially intact specimens into 24 population samples (as defined in table 39), all of which contain only adults. Descriptive statistics for each sample are listed in appendix E, and the specimens measured are identified in appendix F. Our multivariate analyses of these 24 samples focus only on cranial and dental measurements. Lengths of head and body, tail, hind foot, and ear are summarized for only a few samples (table 37) and are used primarily to supplement our qualitative descriptions of each species.

Following the gazetteer are the accounts of species, beginning with *O. nitidus*. There we provide a description of its geographic range, summarize reliable habitat information, describe the species, and present qualitative and quantitative comparisons between *O. nitidus* and the other species in the group. Accounts of *O. macconnelli*, the new species from Pará, and *O. russatus* follow and contain descriptions of the geographic distributions, summaries of habitat information, and morphological and other characteristics. The association of scientific names with each species is documented in Taxonomic Summary.

GAZETTEER AND SPECIMENS

Listed below are the localities at which the 921 specimens we identify as *Oryzomys macconnelli* (total, 264), *O. nitidus* (total, 439), *O. russatus* (total, 201), and the new species from Pará, Brazil (total, 17; identified as the ‘‘Pará Sample’’ in the gazetteer) were collected. The number preceding each place corresponds to the same numbered locality on the maps in figures 78 and 79. We do not list any material that we did not personally examine.

ORYZOMYS MACCONNELLI

FRENCH GUIANA

Arrondissement Cayenne

1. **Arataye** (spelled Arataï in USBGN French Guiana, 1993: 7; ‘‘Réserve de l’Arataye’’ is written on skin labels; includes ‘‘River Arataye,’’ the notation on tags tied to skins of USNM specimens); specimens taken at Saut Pararé, an ‘‘Ecological Station of the Museum National d’Histoire Naturelle,’’ on the left side of the Crique (River) Arataye, 04°02′N/52°42′W (Dubost, 1988: 108), 40 m (Voss and Emmons, 1996: 95): MNHN

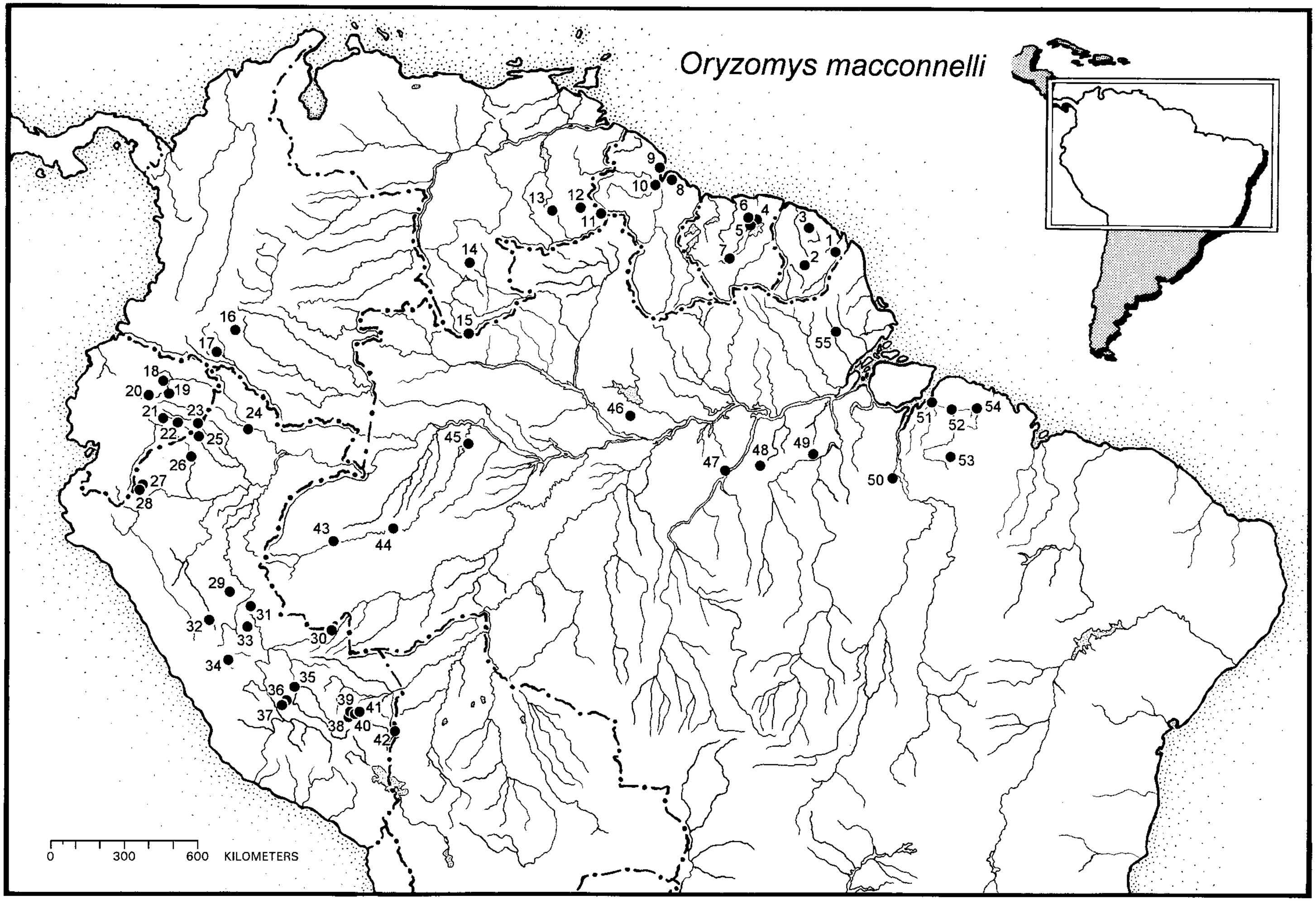

Fig. 78. Distribution of *Oryzomys macconnelli* (based on collection localities for the 264 specimens examined), which conforms to Amazonia (compare with map of Amazonia in fig. 15). Numbers index localities in gazetteer for *O. macconnelli*.

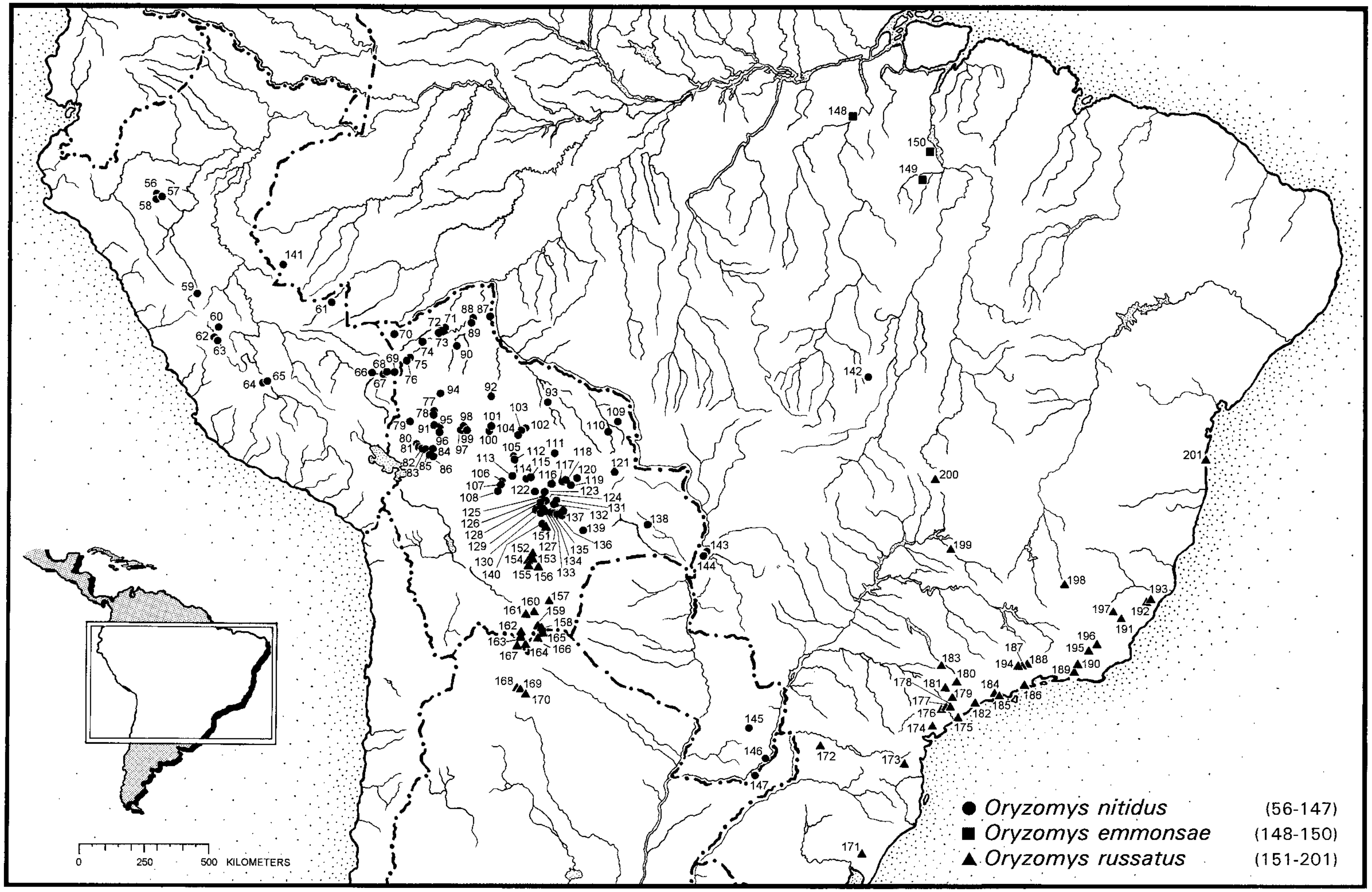

Fig. 79. Distribution of *Oryzomys nitidus* (based on 439 specimens examined), *O. emmonsae*, new species (drawn from 17 specimens examined), and *O. russatus* (based on 201 specimens studied). Numbers refer to localities in the *O. nitidus* group gazetteer.

1983-371–1983-373, 1986-276; USNM 548449, 578018.

2. **Saül**, ‘‘on upper Crique Grande Inini’’ (Stephens and Traylor, 1985: 15), 03°37′N/53°12′W, 200 m: MNHN 1983-365, 1983-367.
3. **Saint-Eugène**, on the Rivière Courcibo (also spelled Koursibo), 04°51′N/53°04′W (from USBGN French Guiana, 1983: 110): MNHN 1994-126, 1994-127, 1995-208.

SURINAM

District Brokopondo

4. **Brownsberg Nature Park** (Stephens and Traylor, 1985: 70, listed the Reserve at 04°55′N/55°12′W), **3 km S and 20 km W Afobakka** (spelled Afobaka in USBGN Surinam, 1993), 04°58′N/55°10′W (coordinates are for the locality, not Afobakka, and come from Genoways et al., 1981: 320): CM 54056–54058. **10 km S and 23 km W Afobakka:** CM 54059.
5. **Brownsberg, western shore of Brokopondo Lake** (Professor Doctor Ingenieur W. J. van Blommestein Meer), 500 m (Husson, 1978: 392): RMNH 20539.
6. **Finisanti, Saramacca River,** 05°08′N/55°29′W (for Finisanti; USBGN Surinam, 1993: 35): FMNH 95595.
7. **1.5 km W Rudi Kappelvliegveld** (= Rudi Kappel Airfield)**,** 03°47′N/56°10′W, 330 m: CM 64561.

GUYANA

District Demerara

8. **Bonasika River** (‘‘West Demerara-Essequibo Coast,’’ Stephens and Traylor, 1985: 25), which is a ‘‘tributary of lower Essequibo River entering on right bank near mouth’’ (Stephens and Traylor, 1985: 25), 06°45′N/58°30′W: BMNH 12.6.5.23.
9. **Supenaam River** (spelled ‘‘Supinaam’’ on skin tags; ‘‘enters mouth of Essequibo . . . from west,’’ Hershkovitz, 1960: 563), 06°59′N/58°31′W (see Stephens and Traylor, 1985: 58): BMNH 10.5.4.29–10.5.4.33, 10.5.4.34 (holotype of *Oryzomys macconnelli*).

District Mazaruni-Potaro

10. **Kartabu Point** (= Kartabo on skin tags), which is ‘‘at Junction of Cuyuni and Mazaruni rivers,’’ Stephens and Traylor, 1985: 38), 30–50 ft, 06°23′N/58°42′W: AMNH 64138.

VENEZUELA

Estado de Bolívar

11. **San Ignacio de Yuruaní, Gran Sabana,** 05°02′N/61°06′W, 850 m: MHNLS 7831, 7836; USNM 448584–448586. **5.2 km NE San Ignacio de Yuruaní** (on road to La Toma de Agua), 850 m: AMNH 257236–257238; MHNLS 8048, 8075, 8076, 8078, 8088.
12. **Kanavayén** (‘‘Kavanayen’’ on skin labels), in ‘‘central eastern Bolívar, 120 km S of El Dorado’’ (Paynter, 1982: 13), 05°38′N/61°48′W, 3300 ft: AMNH 176364, 176365.
13. **Auyán Tepuy,** a ‘‘very large sandstone table mountain, with summit area of 700 sq. km and 200 sq. km. of talus slopes, in east-central Bolívar, on right side of Río Cornoní’’ (Paynter, 1982: 13; also see Tate, 1938, and Gilliard, 1941, for descriptions of the region and collection camps), 05°45′N/62°30′W, 460 and 1100 m: AMNH 130877, 130880, 130882, 130908, 130911, 130913, 130920, 130926, 130928, 130931, 130958, 130961, 130970, 130971, 130974–130976, 130983, 131098, 131100, 131102, 131111, 131119, 131121, 131128, 131131.

Estado de Amazonas

14. **Cerro Duida, Cabecera del Caño Culebra, 40 km NNW Esmeralda,** 03°30′N/65°43′W (Handley, 1976: 65), 1400 m: USNM 406044.
15. **Cerro de la Neblina,** ‘‘a large table mountain of ca. 600 sq/km in southern Amazonas on Brazilian frontier, ca. 250 km S of Cerro Duida and W of Sierra Imeri’’ (Paynter, 1982: 103), 00°50′N/66°00′W, 5000 ft: AMNH 246136.

COLOMBIA

Departamento de Caquetá

16. **La Morelia** (La Murelia is printed on skin label), **Río Bodoquera**, which is ‘‘a hacienda two days’ journey southeast of Florencia in the virgin forest which everywhere covers this part of Colombia’’ (Chapman, 1917: 648 and map frontispiece), 01°30′N/74°48′W (estimated from Chapman’s map), 600 ft: AMNH 33756 (holotype of *Oryzomys incertus* Allen, 1913: 598, which was renamed *Oryzomys mureliae* Allen, 1915: 630).

Departamento de Putumayo

17. **Río Mecaya, at the Río Caquetá** (see Paynter and Traylor, 1981: 157), 00°28′N/75°20′W, 185 m: FMNH 72041, 72061.

ECUADOR

Provincia de Napo

18. **San José Abajo** (this is the notation on skin labels [translates Lower San José]; Chapman, 1926: 719, referred to the place as ‘‘San José de Sumaco’’; Paynter and Traylor, 1977: 110, also explained ‘‘that all American Museum specimens recorded from ‘San

José' or 'below San José' are from or near San José de Sumaco''), 00°26′S/77°20′W, 250 m: AMNH 64018, 68182, 68183.

19. **Río Suno,** which is a ''small tributary of upper Río Napo, rising W of Volcán Sumaco and flowing around northern side and then ca. 60 km E to meet the Napo'' (Paynter, 1993: 201), 00°42′S/77°08′W: AMNH 64017. **Near Río Suno,** 3000 ft: MCZ 27374.
20. **Near Río Napo** (Paynter, 1993: 135, noted that ''the numerous specimens from 'Napo,' 'upper Napo,' etc., may be from anywhere along the river, from Puerto Napo, or from the general area''), 01°03′S/77°47′W (for Puerto Napo, Hershkovitz, 1977: 927), 2400 ft: MCZ 27375.

Provincia de Pastaza

21. **Río Capahuari,** a tributary of the Río Pastaza, 01°55′S/77°20′W (Hershkovitz, 1960: 565), or ''left-bank tributary of middle Río Pastaza meeting that river near Ecuador/Perú border, 02°31′S76°51′W'' (Paynter, 1993: 28): FMNH 43266, 43267, 43272–43275.
22. **Río Bobonaza at Montalvo** (This river is a ''left-bank tributary of Río Pastaza rising at base of mountains near Puyo and flowing past Sarayacu and Montalvo [02°04′S/76°58′W] to meet the Pastaza at the Ecuador/Perú boundary''; Paynter, 1993: 21): FMNH 41455–41457.
23. **Río Tigre,** ''a town on Ecuador-Perú border where Río Conambo and Río Pindo join to form Río Tigre, a major tributary of the Amazon'' (Paynter and Traylor, 1977: 103), 02°07′S/76°04′W, 1000, 1500, and 2000 ft: BMNH 54.445, 54.447–54.450, 54.455–54.459.

PERÚ

Departamento de Loreto

24. **Boca del Río Curaray** (see Stephens and Traylor, 1983: 64), 02°22′S/74°05′W, 140 m: AMNH 71553, 71576–71583, 71585–71588.
25. **Teniente López** (includes 1.5 km N), on left bank Río Corrientes, 02°35′S/76°06′W (Duellman and Mendelson, 1995, provided coordinates, maps, and descriptions of sites at and near Teniente López), below 500 m: NW 858, 870, 871, 881, 879; RMT 4080, 4085, 4087.
26. **Huachi**, which is on the Río Pastaza, 03°25′S/76°20′W (from Hershkovitz, 1977), 1500 ft: BMNH 54.442, 54.451–54.454, 54.471.

Departamento de Amazonas

27. **Río Cenepa, 0.5 mi W Huampami**, 04°35′S/78°12′W (see Stephens and Traylor, 1983: 39): MVZ 153516.
28. **Headwaters Río Kagka,** which is a tributary of the Río Cenepa, 04°26′S/78°17′W, 2600 ft: MVZ 154972, 154974.

Departamento de Ucayali (formerly part of Departamento de Loreto; ''in 1980 the former department of Loreto was divided into two departments, Loreto in the north and Ucayali in the south,'' Stephens and Traylor, 1983: iv)

29. **59 km W Pucallpa,** 08°23′S/74°32′W (for Pucallpa, which is ''on left bank of Río Ucayali,'' see Stephens and Traylor, 1983: 169), 150 m: USNM 461268, 461269.
30. **Balta**, a ''small Cashinahua Indian Village on the Río Curanja, a tributary of the Río Alto Purús'' (Gardner and Patton, 1976: 42; see Voss and Emmons, 1996: 104, as well as Duellman and Thomas, 1996: 3, for a general description of the Balta site), 10°06′S/71°14′W, 300 m: LSUMZ 14366.

Departamento de Huánuco

31. **Aguas Calientes** (''Agua Caliente'' on skin label), ''on Río Pachitea, ca. 20 km above confluence with Río Ucayali'' (Stephens and Traylor, 1983: 3), 08°50′S/74°41′W, 150 m: FMNH 55406.
32. **Éxito** (''Hacienda Éxito'' on skin labels), ''on Río Cayumba, left bank of Río Huallaga tributary'' (Stephens and Traylor, 1983: 70), 09°26′S/76°00′W, 3000 ft: FMNH 24568–24572, 24575, 24577; MCV 27020.
33. **Cerros del Sira** (SW foothills), 09°30′S/74°47′W, 860 m: AMNH 241641.

Departamento de Junín

34. **Perené** (= Colonia del Perené or Perení), a ''coffee plantation at junction of Ríos Paucartambo and Chanchamayo'' (Stephens and Traylor, 1983: 161), 10°58′S/75°13′W: BMNH 0.7.7.31 (800 m), 23.10.6.5 (900 ft).

Departamento de Cuzco

35. **Kiteni** (''66 km beyond Rosalina on road from Quillabamba'' on skin label; a ''small village on Río Urubamba, 66 km by road downriver from Rosalina,'' Stephens and Traylor, 1983: 106), 12°20′S/72°50′W, 1500 ft: LSUMZ 19280.
36. **Río Cosireni**, ''tributary to left bank of Río Urubamba; originates in confluence of Río San Miguel and Río Pampaconas'' (Stephens and Traylor, 1983: 61), 12°33′S/73°04′W, 3000 ft: USNM 194884.
37. **Río San Miguel**, a ''tributary of Río Cosireni . . . near San Fernando'' (Stephens and Traylor, 1983: 195), 12°43′S/73°14′W, 4500 ft: BMNH 22.1.1.33; USNM 194564.
38. **Cadena**, ''in Río Marcapata valley; Kali-

nowski's farm, usually called Hacienda Cadena in the literature'' (Stephens and Traylor, 1983: 25), 13°24′S/70°43′W, 1000 m: FMNH 66395–66397, 68633, 68634.

39. **Huajyumbe**, ''near Quince Mil on Río Marcapata'' (Stephens and Traylor, 1983: 86), 13°15′S/70°35′W, FMNH 84320.
40. **Quincemil** (also spelled Quince Mil), which is ''on left bank of Río Marcapata'' (Stephens and Traylor, 1983: 180), 13°16′S/70°38′W, 680 m: FMNH 75268, 75271, 75274–75279.
41. **40 road km E Quincemil on Río Marcapata,** 13°15′S/70°25′W (estimated): LSUMZ 19276.

Departamento de Puno

42. **Pampa Grande, below San Ignacio on the Río Tambopata**, 14°01′S/68°57′W (for San Ignacio, see USBGN Perú, 1955: 488 [from maps trying to find one of Sanborn's, 1953, records, A. L. Gardner came up with 13°49′S/68°59′W for Pampa Grande]), 3000 ft: FMNH 79900, 79901.

BRAZIL

Estado do Amazonas

43. **Seringal Condor, left bank Rio Juruá,** 06°45′S/70°51′W, below 400 m: JLP 15548, 15549, 15563, 15600, 15619; MNFS 529, 530, 548–550, 563.
44. **Barro Vermelho, left bank Rio Juruá,** 06°28′S/68°46′W, below 400 m: JLP 15859, MNFS 747.
45. **Lago Vai-Quem-Quer, right bank Rio Juruá,** 03°19′S/66°01′W, below 400 m: JUR 355, 393.
46. **80 km N Manaus** (see Malcolm, 1988), 02°25′S/59°50′W, below 200 m: USNM 580004–580007.

Estado de Pará

47. **19 km S Itaituba at Km 19 between Itaituba and Jacaréacanga on the Trans-Amazonian Highway,** 04°17′S/55°59′W, below 200 m: USNM 461784, 461785, 545293, 545294.
48. **South of Santarém at Km 217 on Route BR 165** (which connects Santarém with Cuiabá), 04°00′S/54°40′W, 0–100 m: USNM 544606–544623.
49. **54 km S and 150 km W Altamira** (Gleba 61 Lote 2), 03°40′S/52°45′W, below 200 m: USNM 521438, 521533–521535.
50. **73 km N and 45 km W Marabá, near Pôrto Jatobal** (on the Trans-Amazonian Highway), 04°41′S/49°32′W, below 200 m: USNM 519772–519774, 519776, 521437.
51. **Belém, Utinga** (a suburb of Belém, Paynter and Traylor, 1991: 66) 01°27′S/48°29′W, 0–100 m: USNM 394202.
52. **Capim** (Km 93 and 94 on Route BR 14), 01°41′S/47°44′W, 0–100 m: AMNH 188967, 203403–203415.
53. **150 mi SE Belém**, 0–100 m: AMNH 188968.
54. **Igarapé-Assu,** 01°32′S/47°03′W, 50 m: BMNH 4.7.4.65, 4.7.4.66, 4.7.4.107.

Estado do Amapá

55. **Serra do Navio, Rio Amapari**, 00°59′N/52°03′W, 0–100 m: USNM 394203–394212, 394214–394222, 394224–394230, 394232, 543354–543356.

ORYZOMYS NITIDUS

PERÚ

Departamento de San Martín

56. **Yuracyacu** (''Yurac Yacu'' on skin labels; R. W. Hendee, the collector, noted that ''Yurac Yacu is a rather large village at the junction of the Yurac Yacu stream with the Rio Mayo. It is 35 miles east of Jumbilla on the opposite side of the mountains, and a little over 20 miles W.N.W. of Moyobamba. . . . The altitude is 2500′. . . . Heavy forest occurs close round the village''. [Thomas, 1927a: 361]. This is not the ''Yuraccyacu'' of Gardner and Patton [1976: 43] and Stephens and Taylor [1983: 238], which is located in Departamento de Ayacucho. 05°57′S/77°11′W (USGBN Peru, 1989: 862): BMNH 27.11.1.109.
57. **Moyobamba**, ''on upper Río Mayo (Stephens and Traylor, 1983: 139), 06°03′S/76°58′W, 2800 ft: FMNH 19380, 19389; USNM 259606.
58. **Rioja**, ''ca. 20 km W of Moyobamba'' (Stephens and Traylor, 1983: 184), 06°05′S/77°09′W, 842 m: FMNH 19793.

Departamento de Huánuco

59. **Chinchavito**, ''right bank of Río Huallaga, ca. 22 km upstream from Tingo Maria'' (Stephens and Traylor, 1983: 48), 09°29′S/75°55′W, 3000 ft: BMNH 27.11.1.104–27.11.1.106.

Departamento de Ucayali

60. **Balta** (see locality 30): LSUMZ 12333–12347, 14356, 14357, 14365, 16690, 16691, 16694; MVZ 136573, 136574, 136576, 136578, 136588, 136616.

Departamento de Pasco

61. **Eneñas** (see Stephens and Traylor, 1983: 69), 10°45′S/75°14′W, 5000 ft: BMNH 28.5.1.10.

Departamento de Junín

62. **2 mi NW San Ramón** (San Ramón is located ''where Río Palca and Río Tulumayo join to form Río Chanchamayo,'' Stephens

and Traylor, 1983: 197), 11°08′S/75°20′W (for San Ramón), 2900 ft: AMNH 231682. **2.5 mi W San Ramón**: AMNH 230934.

63. **Amable María**, ‘‘a small community in the Tulumayo Valley about 10 kilometers south of San Ramón and separated by a series of ridges from the Río Tulumayo, which lies to the east’’ (Gardner and Patton, 1976: 42; they also detailed the historic confusion associated with the location of Amable María), 11°10′S/75°19′W: BMNH 85.4.1.9, 85.4.1.10a, 85.4.1.10b, 85.4.1.41 (holotype of *Oryzomys laticeps nitidus*).

Departamento de Ayacucho

64. **San José, on Río Santa Rosa**, ‘‘a small settlement a short distance below Huanhuachayo on the Río Santa Rosa’’ (Gardner and Patton, 1976: 43), 12°44′S/73°46′W, 1000 m: LSUMZ 16693.
65. **Hacienda Luisiana**, ‘‘left bank of Río Apurímac’’ (Stephens and Traylor, 1983: 122), 12°39′S/73°44′W, 500 m: LSUMZ 16662, 16663, 16665.

Departamento de Madre de Dios

66. **Boca Río Inambari** (at confluence with Río Madre de Dios; see Stephens and Traylor, 1983: 98), 12°41′S/69°44′W: FMNH 84316.
67. **7 km W Puerto Maldonado on Río Tambopata** (Puerto Maldonado is ‘‘at confluence of Ríos Tambopata and Madre de Dios,’’ Stephens and Traylor, 1983: 173), 12°36′S/69°11′W (for Puerto Maldonado): USNM 390113, 390114.
68. **4 and 4.5 km W Puerto Maldonado on Río Tambopata**: USNM 390065, 390068.
69. **Reserva Cuzco Amazónico**, ‘‘a wildlife reserve along the north bank of the Río Madre de Dios, 14 km east of Puerto Maldonado, Tambopata Province’’ (Woodman et al., 1995: 3; see also Duellman and Koechlin, 1991), 12°33′S/69°03′W, 200 m (specimens were collected 15 km E and NE of Puerto Maldonado): KU 144458–144462, 144464–144468, 144470, 144471, 144474, 144475, 144477, 144480, 144481, 144484, 144487–144493, 144495, 144497, 144499, 144500, 144502–144505, 144507, 144508, 144510, 144511, 144513–144517.

BOLIVIA

Unless otherwise indicated, coordinates for most localities were taken from the gazetteer in Anderson’s (1997) report on the mammals of Bolivia.

Departamento de Pando

70. **Río Nareuda**, 11°18′S/68°46′W: AMNH 248991, 248992.
71. **Bella Vista**, 11°23′S/67°12′W, 170 m: AMNH 262948.
72. **La Cruz,** 11°24′S/67°13′W, 170 m: AMNH 262962, 262963.
73. **Independencia**, 11°26′S/67°34′W, 170 m: AMNH 262960; MSB 57119.
74. **Palmira**, 11°42′S/67°56′W, 180 m: AMNH 262964, 262965; MSB 57116, 57117.
75. **Santa Rosa**, 12°13′S/68°24′W, 180 m: AMNH 262967.
76. **Isla Gargantua**, 12°23′S/68°35′W, 180 m: AMNH 262961.

Departamento de La Paz

77. **Río Beni**, 14°01′S/67°31′W, 240 m: AMNH 262066, 262106–262108.
78. **Río Beni**, 14°16′S/67°32′W, 240 m: AMNH 262103–262105.
79. **17 km N Apolo**, 14°34′S/68°28′W, 1000 m: USNM 579255–579257.
80. **Mapiri**, which is ‘‘on upper Río Mapiri, 110 km NE of Lago Titicaca’’ (Paynter, 1992: 87), 15°15′S/68°10′W, 800 m: BMNH 1.1.1.63, 1.1.1.64 (holotype of *Oryzomys boliviae*).
81. **San Carlos**, about ‘‘15 km S of Mapiri in western central La Paz’’ (Paynter, 1992: 23), 15°24′S/68°11′W, 1200 m: BMNH 1.2.1.17.
82. **Chimate** (also spelled Chimati), ‘‘presumably in western central La Paz in vicinity of Sarampiuni’’ (Paynter, 1992: 31), 15°25′S/68°00′W (from Anderson, 1997; Paynter gives 15°25′S/68°07′W for Sarampiuni), 700 ft: BMNH 1.2.1.18.
83. **Guanay**, a ‘‘Small, neatly laid out village at junction of R. Tipuani and the Mapiri’’ (G.H.H. Tate’s field journal, AMNH Mammalogy Archives), 15°28′W/67°52′W, 1800 ft (also from Tate’s journal): AMNH 72636–72640.
84. **1 mi W Puerto Linares**, 15°29′S/67°31′W: MSU 33013–33017.
85. **4 km NW (by road) Aloche**, 15°40′S/67°42′W: UMMZ 126775.
86. **La Reserva**, 15°43′S/67°31′W, 840 and 950 m: AMNH 264722–264724, 264730–264767; MSB 68450–68461, 68463–68472.

We also examined BMNH 1.2.1.19 from Carampioni, 800 m, but could not locate the place. It is probably near San Carlos (locality 81) because P. O. Simons, the collector, stopped there on October 8, 1900 and had been at Carampioni on October 2.

Departamento del Beni

87. **Río Mamore, Guayaramerin**, 10°49′S/65°25′W: AMNH 211728.

88. **10 km NNE Riberalta**, 10°55′S/66°02′W: USNM 390661–390663.
89. **Riberalta**, which is in ‘‘northern El Beni, on right bank of Río Beni just below confluence of Río Madre de Dios’’ (Paynter, 1992: 116), 10°59′S/66°06′W, 160 m: USNM 390659, 390660.
90. **Boca del Río Biata**, 11°44′S/66°47′W, 170 m: AMNH 962847–262850, 262949, 262954, 262955, 262958; MSB 57168, 57353, 57354.
91. **Río Beni**, 13°27′S/67°21′W, 240 m: AMNH 262109, 262115.
92. **Río Yacuma, 2 km from mouth**, 13°38′S/65°25′W: AMNH 211731.
93. **Lago Victoria**, 13°46′S/63°30′W: FMNH 117110, 117111, 117113, 117114.
94. **Rurrenabaque**, 14°28′S/67°34′W: AMNH 247781. **3 km S Rurrenabaque**, 14°30′S/67°34′W, 250 m: AMNH 262059–262062.
95. **45 km (by road) N Yacuma**, 14°42′S/67°04′W: AMNH 262051, 262052, 262054, 262056–262058, 262095, 262096; MSB 56055–56057, 56064.
96. **35 km NW Yucumo** (= Yacuma), 14°52′S/67°07′W, 253 m: MSB 68448, 68449.
97. **Estación Biológica del Beni**, 14°51′S/66°21′W, 300 m: AMNH 262049.
98. **Campamento El Trapiche**, 14°48′S/66°19′W, 200 m: AMNH 263494. **2 km E Campamento El Trapiche**, 14°48′S/66°18′W: AMNH 263499.
99. **Río Matos, 6 km E Estación Biológica del Beni**, 14°51′S/66°17′W, 300 m: MSB 56050.
100. **San Ignacio**, 14°53′S/65°36′W: USNM 390062, 390063. **San Ignacio, road to airport**: USNM 390058, 390059. **1 km SW San Ignacio**: USNM 390060, 390061.
101. **3.6 km NNE San Ignacio**, 14°51′S/65°35′W: USNM 390054–390057.
102. **6 km W Casarabe**, 14°54′S/64°22′W, 230 m: AMNH 255955.
103. **Casarabe**, 14°48′S/64°14′W, 230 m: AMNH 262094.
104. **San Andrés,** 15°00′S/64°30′W: FMNH 117102.
105. **Río Mamoré, 5 km NW boca del Río Grande**, 15°50′S/64°41′W: AMNH 211746.

Departamento de Cochabamba

106. **San Antonio del Chimoré** (‘‘San Antonio, Rio Chimoré’’ on skin label), ‘‘on Río Chimoré, northeastern Cochabamba’’ (Paynter, 1992: 122), 16°43′S/65°07′S: AMNH 38524.
107. **Todos Santos**, ‘‘in lowlands of northeastern Cochabamba, on upper Río Chaparé’’ (Paynter, 1992: 151), 16°48′S/65°08′W, 1300 ft: AMNH 38560, 38562.
108. **2 km E Villa Tunari**, 16°57′S/65°23′W, 300 m: AMNH 247779.

Departamento de Santa Cruz

109. **National Park Noel Kempff Mercado, 17 km S Los Fierros**, 14°33′S/60°49′W: MSB 70698.
110. **‘‘El Refugio,’’ Río Paragua**, 14°45′S/61°01′W, 180 m: AMNH 268973–268975.
111. **6 mi (by road) W Ascención**, 15°43′S/63°09′W, 240 m: AMNH 262045, 262046; MSB 56062.
112. **2 km N boca del Río Chaparé,** 15°57′S/64°41′W: AMNH 211716, 211741, 211742.
113. **Río Ichilo, 54 km S boca Río Chaparé**, 16°29′S/64°44′W: AMNH 211732, 211733, 211735–211738.
114. **Punta Rieles, Río Yapacani**, 16°35′S/64°12′W: AMNH 263367, 263368.
115. **Yapacani**, 16°32′S/63°59′W (from skin labels): BMNH 84.1748–84.1750, 84.1752, 84.1753.
116. **Estancia Cachuela Esperanza**, 16°47′S/63°14′W, 300 m: AMNH 260353–260357, 260359–260364, 260412; MSB 55328–55334.
117. **Río Quizer**, 16°37′S/62°46′W, 800 m: CM 5019.
118. **10 km N San Ramón**, 16°36′S/62°42′W, 250 m: AMNH 262043, 262044, 262093; MSB 56073.
119. **Palmarito, Río San Julián**, 16°49′S/62°37′W, 400 m: CM 4980–4982, 4987, 4988, 4990, 4994.
120. **14 km NE San Ramón**, 16°35′S/62°25′W, 540 m: AMNH 264181.
121. **San Ignacio de Velasco**, 16°23′S/60°59′W: USNM 390069–390071.
122. **Ayacucho**, 17°00′S/63°55′W, 250 m: AMNH 263341.
123. **7 km N Santa Rosa**, 17°03′S/63°35′W: AMNH 254600.
124. **Río Surutú**, ‘‘a headwater of Río Yapacani rising SW of Buena Vista, central western Santa Cruz’’ (Paynter, 1992: 142; specimens were obtained by J. Steinbach, and Paynter claimed that his material from the Río Surutú probably came from near Buenavista), 17°22′S/63°25′W, 450 and 500 m: CM 2182–2184, 4965, 4966, 5037.
125. **6 km N Buen Retiro**, 17°13′S/63°38′W, 300 m: AMNH 260352.
126. **Buenavista** (also spelled Buena Vista), which is ‘‘in central western Santa Cruz in Provincia Ichilo, on Río Surutú, 64 km NW of city of Santa Cruz’’ (Paynter, 1992: 13), 17°27′S/63°40′W, 450 and 500 m: CM 2193, 4932.

127. **San Rafael de Amboró**, 17°36′S/63°36′W, 400 m: AMNH 262024, 262026, 262027, 262030–262036, 262038, 262039, 262068, 262074, 262075, 262078, 262098, 262365; MSB 56360, 56362, 56064–56070.
128. **3 km N and 13.5 km W San Rafael de Amboró, Río Saguayo**, 17°34′S/63°48′W, 450 m: AMNH 262083, 262087–262089.
129. **Hunting camp 4 km S and 13 km W San Rafael de Amboró,** 17°39′S/63°48′W: AMNH 263189.
130. **4.5 km N and 1.5 km E Cerro Amboró, Río Pitasama**, 17°45′S/63°40′W, 620 m: AMNH 262040, 262042, 262082; MSB 56063.
131. **La Abra, 18 km NE Warnes**, 17°22′S/63°02′W: USNM 390101–390105.
132. **Warnes**, 17°30′S/63°10′W, 1200 ft (Paynter, 1992: 164): USNM 390074–390100. **Santa Rosita, 3 km SW Warnes**, 17°31′S/63°11′W: USNM 390072, 390073.
133. **6 km W Santa Cruz**, 17°48′S/63°13′W: USNM 390657, 390658.
134. **2 and 3 km SW Estancia Las Cruces**, 17°47′S/63°22′W, 480 m: AMNH 263873–263879; MSB 63356–63358.
135. **15 km S Santa Cruz**, 17°53′S/63°07′W, 400 m: MSB 50644.
136. **27 km SE Santa Cruz**, 17°58′S/63°03′W, 365 m: MSB 59877–59882.
137. **3.5 km W Estación Pailón**, 17°39′S/62°45′W, 300 m: AMNH 260366–260372; MSB 55335, 55337.
138. **4 km N and 1 km W Santiago de Chiquitos**, 18°18′S/59°36′W, 400 m: AMNH 260373–260376; MSB 55337–55339.
139. **8 km SE Tita**, 18°28′S/62°07′W, 290 m: AMNH 260377.
140. **1 km (Hwy Km 101) NE Estancia Las Cuevas**, 18°11′S/63°44′W, 1300 m: AMNH 264183; MSB 67322, 67323, 70697.

We also examined other specimens collected in Departamento de Santa Cruz but omitted the localities from the map in figure 79. Several are from **Cerro Hosáne**, collected by J. Steinbach in August, 1917 (CM 4935, 4936, 4940, 4946, 4949, 4950, 4952, 4959; 1200 and 1300 m). We could not locate that place. Material obtained by Steinbach came from ‘‘W of Buena Vista’’ according to Paynter (1992: 62). Anderson (personal commun.) was also unable to locate the Cerro and told us it was probably one of the high points in the hills south and west of Buenavista that form the beginnings of the Andean foothills.

BRAZIL

Estado do Acre

141. **Igarapé Porongaba, right bank Rio Juruá**, 08°40′S/72°47′W, below 400 m: MNFS 1147, 1223, 1309, 1419, 1420.

Estado do Mato Grosso

142. **Serra do Roncador, 264 km (by road) N Xavantina** (biological and geographic information about this site are provided in Pine et al., 1970, Askew et al., 1970, Ratter et al., 1973, and Bishop, 1974), 12°49′S/51°46′W (from Pine et al., 1970), 400 m: BMNH 81.436.

Estado de Mato Grosso do Sul

143. **10 km NE Urucum on San Marcus Road**: USNM 390110.
144. **Urucum**, which is ‘‘18 km SSE of Corumbá’’ (Paynter and Traylor, 1991: 659), 19°09′S/57°38′W, 971 m: FMNH 26786 (‘‘Urucum de Corumba’’ on skin label); USNM 390109 (‘‘22 km S Corumbá’’ on skin label).

PARAGUAY

Departamento de Caagazú

145. **Colonia Somerfield** (‘‘Summerfield Colony #11’’ on skin tag), 25°26′S/55°43′W (USBGN Paraguay, 1992: 20): USNM 293147.

Departamento de Itapúa

146. **2 km NNW Puerto San Rafael** (= San Rafael)**, Arroyo San Rafael**, ‘‘in northeastern Itapúa, on Río Paraná’’ (Paynter, 1989: 39), 26°40′S/54°53′W: UMMZ 126008.

ARGENTINA

Provincia de Misiones

147. **Puerto Gisela**, which is on Río Paraná, 18 km NE Corpus, southern Misiones (Paynter, 1985: 312), 27°01′S/55°27′W, 50 m: BMNH 24.6.6.42.

THE PARÁ SAMPLE

BRAZIL

Estado de Pará

148. **E Bank Rio Xingu, 52 km SSW Altamira,** 03°39′S/52°22′W, below 100 m: MZUSP 27150; USNM 549551, 549552.
149. **Marabá, Serra Norte,** 06°00′S/50°20′W: USNM 543327–543338.
150. **73 km N and 45 km W Marabá, near Pôrto Jatobal** (on the Trans-Amazonian Highway), 04°41′S/49°32′W, below 200 m: USNM 519775, 521530.

ORYZOMYS RUSSATUS

BOLIVIA

Unless otherwise indicated, coordinates for Bolivian localities were obtained from the gazetteer in Anderson's (1997) report on the mammals of Bolivia.

Departamento de Santa Cruz

151. **1 km (Hwy Km 101) NE Estancia Las Cuevas,** 18°11′S/63°44′W, 1300 m: AMNH 264182, 264184, 264185; MSB 67321.

Departamento de Chuquisaca

152. **Tola Orko, 40 km from Padilla**, 19°27′S/64°07′W, 2100 m: USNM 271584–271587, 545225.
153. **Montecantu** (= Cullpur), 19°31′S/64°09′W, 1985 m: USNM 270914, 271583.
154. **Río Limón**, 19°33′S/64°08′W, 1300 m: AMNH 263881–263885; MSB 63360, 63584.
155. **Tihumayo**, 19°34′S/64°08′W: USNM 290903.
156. **2 km E Chuhuayaco** (= Chuyayacu), 19°43′S/63°51′W, 1200 m: AMNH 263886, 263887; MSB 63359.

Departamento de Tarija

157. **1 km S Camatindi**, 21°00′S/63°23′W, 650 m: AMNH 264186.
158. **Caraparí**, ''on eastern slopes of southeastern Tarija, 20 km W of Caiza'' (Paynter, 1992: 23), 21°49′S/63°46′W, 1000 m: BMNH 25.2.1.24 (holotype of *Oryzomys legatus*), 25.2.1.25.
159. **3 km WNW Caraparí**, 21°48′S/63°47′W, 850 m: AMNH 264190, 264191.
160. **5 km NNW Entre Ríos**, 21°29′S/64°12′W, 1600 m: AMNH 264187–264189.
161. **Tapecua**, 21°26′S/63°55′W, 1500 m: MSB 67318–67320, 67358, 67359.
162. **4 km (by road) N Cuyambuyo, Fabrica del Papel, Río Sidras**, 22°13′S/64°36′W, 980 m: UMMZ 155888.
163. **3 km SE Cuyambuyo**, 22°16′S/64°33′W, 900 m: AMNH 264280.
164. **Monte Bello** (''Río Lipeo'' on skin label), a ''farm in southern Tarija, near Argentina border, near where the Río Lipeo and the Río Candado meet'' (Paynter, 1992: 91), 22°41′S/64°26′W, 2100 ft: ANSP 18189.

ARGENTINA

Provincia de Salta

165. **17 km SW beyond Dique Itiyuro, near Yacuiba** (see maps in Mares et al., 1981b, and Ojeda and Mares, 1989), 22°02′S/63°45′W (for Yacuiba, which Paynter, 1992: 165, noted is on the Argentine–Bolivian border in southern Tarija), 500 m: CM 43827.
166. **Piquirenda** (''Piquirenda Viejo'' on specimen labels, 30 km N Tartagal), 22°20′S/63°47′W, 700–800 m (Paynter, 1985: 300): CM 72391.
167. **24 km NW Agua Blanca** (see maps in Mares et al., 1981b, and Ojeda and Mares, 1989), 22°44′S/64°22′W (for Agua Blanca, Paynter, 1985: 4): CM 43821–43826.

Provincia de Jujuy

168. **2.9 km E El Palmar, Sierra Santa Bárbara**, which is a north–south ridge ''ca. 50 km long, 40 km E of San Pedro, extreme eastern Jujuy'' (Paynter, 1985: 368), 24°05.27′S/64°34.07′W (from skin labels): ARG 3414, 3446, 3449, 3450.
169. **8.4 km E El Palmar, Sierra de Santa Bárbara**, 24°07′S/64°18′W (for Santa Bárbara, Paynter, 1985: 368): ARG 3471.
170. **El Simbolar, 25 km S Palma Sola**, 23°59′S/64°18′W (for Palma Sola, Paynter, 1985: 280): CM 43819, 43820.

BRAZIL

Estado de Rio Grande do Sul

171. **Taquara** (''Taquara do Mundo Novo'' on skull label), ''on coastal plain, 60 km NE of Pôrto Alegre and 6 km S of Mundo Novo'' (Paynter and Traylor, 1991: 625), 29°39′S/50°47′W, 29 m (Voss, 1993: 6, pointed out that Taquara and ''Taquara do Mundo Novo'' are probably the same locality; Mundo Novo, however, is at 29°32′S/50°48′W): UZM 7498 (lectotype of *Hesperomys laticeps* var. *intermedia*).

Estado do Paraná

172. **Salto Grande**, 25°59′S/52°43′W (USBGN Brazil, 1963: 719): USNM 141450.

Estado de Santa Catarina

173. **Corupá** (=''Hansa,'' the name on specimen tags), 26°26′S/49°14′W, 62 m (Paynter and Traylor, 1991: 166): BMNH 28.10.11.21, 29.6.6.48, 29.6.6.49; USNM 236694.

Estado do São Paulo

174. **Estrada do Carijo, Cananéia**, which is ''on Atlantic coast in southernmost part of state'' (Paynter and Traylor, 1991: 118), 25°01′S/47°57′W, 6 m: AMNH 203074 (paratype of *Oryzomys ratticeps moojeni*).
175. **Iguape**, ''on coast of southern São Paulo, behind long narrow barrier island, midway between city of São Paulo and Paraná border'' (Paynter and Traylor, 1991: 287), 24°43′S/47°33′W, sea level: USNM 542929.
176. **Pousinho** (''Rio Juquiá'' also written on tag), ''mountainous area near Rio Juquina, by coast'' (Paynter and Traylor, 1991: 493), 24°22′S/47°49′W: FMNH 93063.
177. **Ribeirão Fundo**, ''settlement in southern São Paulo, NW of Juquía, ca. 16 km N of

Primeiro Morro, on right bank of Ribeirão Fundo, which rises on Sierra de Paranapiacaba and discharges into right side of Rio Juquía'' (Paynter and Traylor, 1991: 517), 24°15′S/47°45′W, 30 m: FMNH 94547, 94554.

178. **Primeiro Morro**, ''16 km NW of Juquiá on left bank of Ribeirão Fundo on coastal plain, first major hill as one ascends Ribeirão Fundo'' (Paynter and Traylor, 1991: 498), 24°19′S/47°38′W (for Juquiá; Paynter and Traylor located a different Primeiro Morro, but not the one we list, which is the source of the FMNH specimens), 25 m: FMNH 94545, 94546.
179. **Rocha**, ''on inland edge of the coastal plain at headwaters of Ribeirão Fundo, ca. 40 km NNW of Juquiá'' (Paynter and Traylor, 1991: 527), 50 m (not located by Paynter and Traylor; dot on our map indicates 40 km NNW Juquiá): FMNH 94548–94550.
180. **Itanhaém**, ''on coast of central São Paulo, 70 km S of city of São Paulo'' (Paynter and Traylor, 1991: 305), 3 m: USNM 542923–542926.
181. **Alambari** (''Alambary'' on skin labels), ''in central western part of state, 130 km W of city of São Paulo'' (Paynter and Traylor, 1991: 9), 23°33′S/47°53′W, 600 m: BMNH 3.7.1.142, 3.7.1.143.
182. **Ipanema** (''Ypanema'' is spelling on specimen labels), ''97 km WSW of São Paulo'' (Paynter and Traylor, 1991: 294), 23°26′S/47°36′W (see Vanzolini, 1993: 27, who provided maps and other materials that reconstruct Natterer's itineraries in Brazil), 600 m (from skin tag of BMNH specimen; Paynter and Traylor give 950 m for Ipanema): BMNH 3.7.1.167; NMW B469, B477, B478 (lectotype of *Hesperomys russatus*), B481.
183. **Vitoriana** (= ''Victoria,'' the name on specimen labels), 22°47′S/48°24′W, 200 m (Paynter and Traylor, 1991: 681): BMNH 2.4.6.26; USNM 141449.
184. **Casa Grande**, ''11 km SW of Sallesópolis and 75 km ESE of São Paulo'' (Paynter and Traylor, 1991: 134), 23°37′S/45°57′W, 1000 m: USNM 461986–461989, 484025–484042, 485001–485003, 485005, 485006, 485010, 485011, 485014–485016, 485018, 485020. **Barragem**, which is ''in the Casa Grande area'' according to Oscar de Souza Lopes, the collector (files in Mammal Division, USNM): USNM 484022–484024, 485004, 485013, 485019.
185. **Rio Guaratuba** (= ''Varjão,'' which is the name on skin labels), a ''coastal research station and possibly village near mouth of Rio Guaratuba and Praia Guaratuba, ca. 75 km ESE of São Paulo'' (Paynter and Traylor, 1991: 523), 23°45′S/45°55′W, sea level: USNM 461985, 485007–485009, 485012, 485017, 485021, 542922, 542927, 542928.
186. **Ubatuba**, ''coastal northeastern São Paulo, 158 km E of city of São Paulo'' (Paynter and Traylor, 1991: 654), 23°26′S/45°04′W, sea level: USNM 304597, 304598.
187. **Piquete**, ''northeastern part of state, in Serra da Mantiqueira, almost on the Minas Gerais border, 180 km NE of São Paulo and 200 km W of Rio de Janeiro'' (Paynter and Traylor, 1991: 467), 22°36′S/45°11′W, 900 m: BMNH 1.6.6.38–1.6.6.42; FMNH 18874, 18875; USNM 172976.
188. **Cruzeiro** (10 km E Rio Parahyba), 22°35′S/44°45′W, (Hershkovitz, personal commun.), 530 m: BMNH 1.2.7.28–1.2.7.35.

Estado do Rio de Janeiro

189. **Magé** (''Municipio Magé, locality C.P.R.J.'' on skin labels), 22°39′S/43°02′W, 100 m (Paynter and Traylor, 1991: 358): BMNH 86.1164–86.1167.
190. **Teresópolis** (''E Rio Terezopolis'' on skin labels), ''in Serra dos Órgãos of the coastal range, central Rio de Janeiro, 58 km NE of city of Rio de Janeiro'' (Paynter and Traylor, 1991: 633; also see Davis, 1945, and Voss, 1993), 22°26′S/42°59′W, 902 m: FMNH 53876.

Estado do Espírito Santo

191. **Rive** (=''Engenheiro Reeve,'' which is on skin labels), ''in southwestern part of state, 38 km WNW of Cachoeiro de Itapemirim'' (Paynter and Traylor, 1991: 526), 20°46′S/41°28′W, 600 m: BMNH 3.9.4.55, 3.9.4.57.
192. **Santa Teresa**, 19°55′S/40°56′W, 659 m (Paynter and Traylor, 1991: 556): USNM 304599, 304600.
193. **Reserva Biológica de Nova Lombardia,** 19°46′–19°55′S/40°30′–40°35′W, 500–1200 m (Paynter and Traylor, 1991: 413): LACM 52159–52161, 52163, 62899.

Estado de Minas Gerais

194. **São Francisco** (''San Francisco'' on skin labels), ''within southwestern part of Serra da Mantiqueira, 25 km SSE of Itajubá and 25 km NW of Lorena, extreme southern part of state'' (Paynter and Traylor, 1991: 570), 22°36′S/45°18′W, 1580 m: BMNH 1.6.6.37, 1.11.3.50.
195. **Fazenda São Geraldo, Além Paraíba**, ''on left bank of Rio Paraíba do Sul 37 km S of Leopoldina and 72 km ESE of Juiz de Fora in extreme southeastern part of state'' (Paynter and Traylor, 1991: 11), 21°52′S/42°41′W, 140 m: AMNH 203073 (paratype of *Oryz-*

omys kelloggi); USNM 304564–304569, 332452 (paratype of *Oryzomys kelloggi*).

196. **Volta Grande**, ‘‘near left bank of Rio Paraíba do Sul, 20 km below Além Paraíba and 85 km E of Juiz de Fora, extreme southeastern Minas Gerais’’ (Paynter and Traylor, 1991: 681), 21°46′S/42°32′W, 215 m: USNM 304562, 304563.
197. **Serra do Caparaó**, which is a ‘‘range ca. 35 km long on the Minas Gerais/Espírito Santo border with highest peak known as Pico da Bandeira,’’ (Paynter and Traylor, 1991: 123), 20°22′S/41°48′W, 3360 ft: AMNH 61835, 61837.
198. **Lagoa Santa**, 19°38′S/43°53′W, 760 m (Paynter and Traylor, 1991: 341; also consult Voss, 1993, and Voss and Myers, 1991, who discussed the cave collections from the Lagoa Santa region): holotype of ‘‘*Calomys coronatus*’’ in paleontological collections of UZM; see discussion in Taxonomic Summary.
199. **Ribeirão Jordão, near Araguari** (‘‘Río Jordão near Araguary’’ on skin tags. Thomas [1901b: 527] noted that Alphonse Robert, who worked near ‘‘Araguary,’’ obtained the collection ‘‘in the tropical forest bordering the Paranahyba [= Rio Paranaíba], and therefore no doubt gives a sample of the fauna running northwards along that river into Goyaz.’’), 18°38′S/48°11′W (for Araguari, Paynter and Traylor, 1991: 28), 900 m: BMNH 1.11.3.29–1.11.3.31, 1.11.3.32 (holotype of *Oryzomys lamia*), 1.11.3.33, 1.11.3.34, 1.11.3.45.

Estado de Goiás

200. **Anápolis**, 16°20′S/48°58 (Paynter and Traylor, 1991: 19), 1000 m: AMNH 134644, 134663–134667, 134763, 134677, 134772, 134680.

Estado da Bahia

201. **Ilhéus**, ‘‘Atlantic port in southern Bahia’’ (Paynter and Traylor, 1991: 289), 14°49′S/39°02′W, sea level: FMNH 63776; KU 39315, 39351; USNM 304572, 304573.

ORYZOMYS NITIDUS (Thomas, 1884)

Thomas (1884: 452–453) described *nitidus* as a new variety of *Hesperomys* (*Oryzomys*) *laticeps* based on ‘‘Eighteen specimens, mostly young’’ from ‘‘Junin’’ and ‘‘Amable Maria.’’ ‘‘These specimens,’’ wrote Thomas,

> are readily separable at sight from the ordinary *H. laticeps*, more resembling *H. albigularis*, Tomes, or *H. vulpinoides*, Schinz, in their general appearance; but a closer examination shows that the points of difference between them and *H. laticeps* are all such as are explainable on ordinary climatic grounds, supposing that their home is hotter than the places in which *H. laticeps* ordinarily lives.
>
> They are characterized by their dark rich rufous colour, apparently pure white bellies, though the hairs are slate-coloured at their bases, longer tails, bicolor for their proximal inch, proportionately longer hind feet, and larger ears. Their skulls are quite similar to those of the true *H. laticeps*. In this variety we have, so to speak, the commencement of a species, which appears to be gradually becoming differentiated from another common and widely-spread form, and which will possibly in the future become more and more distinct from its parent, as the individuals representing the intermediate stages die out, until it is itself worthy to rank as a separate species.

Thomas had not designated a holotype in the report of 1884, but years later did select a lectotype for ‘‘*Oryzomys nitidus*, Thos.’’ (Thomas, 1927b: 549): BMNH 85.4.1.41 (fig. 131; table 49), a young adult male collected by C. Jelski at ‘‘Amable Maria, Central Peru’’ (locality 63 in gazetteer).

Gardner and Patton (1976: 40) included *boliviae* (Thomas, 1901c: 536) and *legatus* (Thomas, 1925: 577) as synonyms of *O. nitidus*, and suggested that *bolivaris* (Allen, 1901: 405) and *intermedius* (Leche, 1886: 693) may also be synonyms. However, our study of holotypes and analyses of cranial and dental measurements indicate that only *boliviae* is an example of *O. nitidus*, and we regard *boliviae* as the only synonym of that species (see Taxonomic Summary).

Both *nitidus* and *boliviae* were included in Hershkovitz’s (1960) footnote that synonymized them with *O. laticeps*. Earlier, Gyldenstolpe (1932: 18) treated *nitidus* as a subspecies of *O. laticeps* but listed *boliviae* as a separate species. Later, Cabrera (1961) listed *nitidus* as a subspecies of *O. capito* and *boliviae* as a subspecies of *O. albigularis*.

By 1976, Gardner and Patton had isolated the morphological and chromosomal traits diagnostic of *nitidus*, treating it as a species. They characterized it this way (p. 39):

> The $2n = 80$, $FN = 86$ animals from Perú are morphologically identical with the holotype of *O. nitidus*; consequently, we are using this name for this species. . . . *Oryzomys nitidus* exhibits these characters: dorsal adult coloration reddish brown, grading on the sides to cinnamon along the lateral line (immatures a mixture of gray and reddish brown dorsally); ears clothed internally and externally with black hairs; in-

cisive foramina comparatively long and narrow; sphenopalatine pits usually simple; palatal excrescences (incipient palatal bridge) present in most individuals; enamel island present in the second upper molars between the medial portion of the first primary fold from the major fold (first internal fold discrete)

The distinction of *O. nitidus* from *O. megacephalus* and other species formerly included in the *O.* ''*capito*'' complex has been accepted from 1976 until the present (see, for example, taxonomic results such as Musser and Williams [1985]; regional faunal reports such as those for Perú by Cadle and Patton [1988], Woodman et al. [1991, 1995], and for Bolivia by Anderson [1997]; and general systematic lists, as exemplified by Pacheco et al. [1993, 1995], and Musser and Carleton [1993]). The boundaries, however, of morphological variation in *O. nitidus* as well as its geographic range have never been formally described.

Our purpose here is to define *Oryzomys nitidus*. In the following pages, we elaborate its geographic distribution as indicated by specimens listed in the gazetteer, summarize ecological data and evidence of sympatry, describe characteristics of the species and contrast them with other species in the *O. nitidus* group, and discuss intraspecific geographic variation.

DISTRIBUTION AND HABITAT

Documented collection localities for *O. nitidus* indicate that the species occurs east of the Andes in Perú and in closely adjacent parts of Brazil and Bolivia, east through central Brazil, and south to southeastern Paraguay and northeastern Argentina (fig. 79). Of the 439 specimens we examined, 432 were collected from places along the eastern Andean foothills and nearby lowlands in Perú, adjacent Brazil, and Bolivia. In this portion of the range, Departamento de San Martín (about 06°S/77°W; locality 56 in gazetteer), north-central Perú, marks the northernmost extent of the species and Departamento de Santa Cruz (18°–19°S/59°–64°′W; localities 138–140), south-central Bolivia, the southernmost extent.

Encounters with the species by collectors have been less frequent in central and southern Brazil, Paraguay, and northern Argentina, a vast region represented by only seven specimens trapped at six localities. Our easternmost record is one example captured in the Serra do Roncador (12°49′S/51°46′W; locality 142), central Brazil. To the south, three specimens were collected near Urucum in the Pantanal of Estado de Mato Grosso do Sul (localities 143 and 144). The southernmost records of *O. nitidus* are two specimens from west of the Río Paraná in eastern Paraguay (localities 145 and 146; Myers, 1982, reported Paraguayan records as *O. intermedius*, as did Martinez, 1996) and a single example collected from the opposite side of the Río Paraná (27°01′S/55°27′W; locality 147) in Provincia de Misiones, Argentina (Massoia, 1974, identified two other specimens from Misiones as ''*Oryzomys* (*Oryzomys*) *capito intermedius*'').

The absence of *O. nitidus* from Brazil north of the Amazon river, as well as from Venezuela and the Guiana Region, is probably real and not an artifact considering the collection efforts of different survey groups working at different times in the region. Nor has the vast core of the Amazon Basin yielded specimens of *O. nitidus*. This area has not been subjected to the same intensive efforts as those devoted to the Guiana Region, but large collections of small mammals have been made in Pará south of the Amazon River (especially near Belém) and in the state of Amazonas along the length of the Rio Juruá; examples of *O. nitidus* have been encountered only at one site, near headwaters of the Rio Juruá (locality 141 in gazetteer). Elsewhere, the species does not occur in nor has it been recorded from the Chaco Boreal of southern Bolivia and western Paraguay, or from eastern Brazil east of the Rio Tocantins in the north or the Rio Paraná in the south.

Elevational records for *O. nitidus* extend from 1524 m along the foothills of the Andes in Perú to about 200 m in Amazonian Brazil and the departments of Pando and Beni in Bolivia, and 50 m in the Argentine province of Misiones.

Compilation of habitat information from field journals, specimen tags, personal trapping experience, and conversation with other mammalogists reveals that *O. nitidus* inhabits tropical and subtropical evergreen humid forests. Although it has been collected in primary forest formations, many collections come from second-growth forest in various stages of regeneration and from the tall shrubby ecotone between open fields and some kind of forest structure. Before human destruction and modification of pristine habitats, *O. nitidus* probably occurred throughout primary forest from the expanse of evergreen formations in western Amazonia south into subtropical (including deciduous) forest associations, as well as along the convolutions of gallery forest through palm savanna and cerrado. The species is similar to *O. megacephalus* and *O. yunganus* in its ability to exploit moderately to severely modified habitats within primary forest, and like those other species, *O. nitidus* seems to be absent from grassland formations. The wide ecological tolerance of *O. nitidus* contrasts with the narrow habitat affinities of its close relative, *O. macconnelli*, which is apparently restricted to primary forest. The habitat data we obtained for *O. nitidus* are summarized below by country.

Perú: Collection localities for *O. nitidus* in Perú, adjacent Brazil, and northern Bolivia are in western Amazonia, a region where tropical evergreen rain forest is the primary vegetative formation (or was before humans modified or removed it). The meager habitat data we located for collection sites in Perú indicate that *O. nitidus* inhabits both secondary and primary forest. At **Balta** (locality 60), for example, A. L. Gardner and J. L. Patton caught most specimens of *O. nitidus* in 4–5-year-old gardens that were converting to second-growth forest on a river terrace. Scattered banana and manioc plants still remained. (General description of the Balta site is provided by Voss and Emmons [1996: 103] and Duellman and Thomas [1996: 3].)

Captures in primary forest are represented by a large series of *O. nitidus* from the reserve at **Cuzco Amazónico** (locality 69), where examples were caught during both dry and wet seasons in ‘‘floodplain forest’’ and ‘‘floodplain forest adjacent to seasonally inundated swamp forest’’ (Woodman et al., 1995: 3). According to Duellman and Koechlin (1991: 10),

> The mostly evergreen tropical forest on alluvial soil in the reserve contains about 400 species of trees. . . . Most of the large trees attain heights of about 30 m and form an incomplete forest canopy. Emergents (including *Ceiba*, *Chorisia*, *Dipteryx*, and *Ficus*) reach heights of 40 m or more. In the midlevel and understory of the forest, the vegetation is rather dense with many woody vines . . .; the nearly 40 lianas (>10 cm diameter) per ha is nearly twice the average for Amazonian forests. . . . Consequently, except in areas of treefalls, little sunlight reaches the forest floor. . . . Palms are common components of the understory. . . . Throughout the forest, the most conspicuous ground cover is ferns. . . . Arboreal bromeliads are scarce, but epiphytic ferns and orchids are moderately common.

Duellman and Koechlin also provided a vegetation profile through the ‘‘floodplain forest adjacent to seasonally flooded forest’’ as well as summary information on rainfall patterns and soils.

Bolivia: Most of the *O. nitidus* we studied and record here were obtained in Bolivia (localities 70–140), but unfortunately we located very little relevant habitat information in collectors’ journals. Given the the general paucity of data about vegetative associations and microhabitats where specimens were captured, we overlaid collection localities on the vegetation map in Hueck and Seibert (1981) to determine what broad vegetational formations are represented by the localities. Bolivia is a mosaic of forested and nonforested areas. In lowlands east of the Andean slopes, the wet tropical evergreen humid forest of Amazonia extends into northern Bolivia where it fragments into broad tongues that gradually constrict into gallery (or riverine) forest. Such ribbons of forest wind south to the central part of the country through extensive regions of palm savanna in northern and central Bolivia, as well as smaller areas of deciduous forest and cerrado in the east and southeast. These mixed landscapes of forest and savanna give way to the semiarid Chaco Boreal and Bolivian Pantanal (‘‘vast areas of semideciduous forest, marsh, and palm savanna,’’ Parker et al., 1993: 13) in southern and southeastern Bolivia. Wet, evergreen lower and upper montane rain forests, the ‘‘yungas,’’ blanket the eastern Andean slopes the length of the country.

Nearly all Bolivian localities at which *O. nitidus* were captured fall within mapped zones of Amazonian evergreen rain forest, riverine forest, or the strip of yungas along the lower Andean slopes. Some of these areas remain forested, but in others the original forest has either been removed or modified by humans. A few collection sites are in palm savanna, the deciduous forest and cerrado formations in eastern Bolivia, and northern boundary areas of the Chaco where it abuts palm savanna and deciduous forest.

Specific habitat information from any particular site is sparse and comes from specimen labels or field notes. Specimens from northeastern Bolivia, a region once covered by tropical evergreen forest, were captured at nonforest or disturbed forest sites. In 1900, for example, P. O. Simons worked at **Mapiri** (locality 80), where he collected a specimen of *O. nitidus* ‘‘in brush,’’ and at **Chimate** (locality 82), where a specimen was taken ‘‘in rice bin’’ (data are from skin labels). Tate (field journal, AMNH Mammalogy Archives) described the habitat around **Guanay** (locality 83) as ‘‘Much deforested close to town and considerable thorny second growth. Farther back forested. Land flat, forming an extensive ‘playa’’’ (April 1926). One *O. nitidus* was caught in ‘‘traps set in second growth forest much intersected by trails, much promenaded by the village pigs, and very much aswarm with ants.’’

Habitat of animals captured during May 1991 at a site in southern Bolivia, **1 km NE of Estancia Las Cuevas** (locality 140), was recorded by collectors (field notes of J. L. Cook, N. S. Cook, M. L. Campbell, J. A. Dunnum, and F. W. Davis; AMNH Mammalogy Archives). On the vegetation map of Hueck and Seibert (1981), this locality falls in gallery forest surrounded by palm savanna, but field notes indicated the forest had been significantly modified. One specimen (MSB 70697) was trapped ‘‘Along edge of soccer field in heavy undergrowth, 15′ canopy, shady, leaf litter, forbes, vines. Cover at shrub and ground 75%, canopy 80%’’; MSB 67322 was captured in ‘‘ecotone, between second growth and soccer field’’ in ‘‘dense shrubs, leaf litter, vines, forbes along trail in small clearing, willow canopy at 30′, canopy cover 40%, ground/shrub cover 90% . . . from a 60° slope with little overgrowth and more grasses and other ground plants’’; MSB 67323 was ‘‘caught on 60° slope, grasses, and no canopy. Thick brush. Clay soil’’; finally, AMNH 264183 was taken in a line of traps ‘‘set between burro pasture and river.’’

Brazil: Forest characterizes most of the few collection localities to the east and southeast of Bolivia. The specimen captured from the region north of Xavantina in the **Serra do Roncador** (locality 142) was trapped in gallery forest along with large samples of *O. yunganus* and *O. megacephalus* (see the descriptive summaries in habitat section for *O. yunganus*; habitat information is from I. Bishop’s field notes in archives of British Museum). Descriptions of vegetation and soils in the Xavantina area, including habitat photographs, forest profiles, vegetation maps, and other illustrative information, were provided in the reports by Askew et al. (1970) and Ratter et al. (1973).

Three specimens were collected near **Urucum** (localities 143 and 144), which is in the Pantanal of western Mato Grosso do Sul, a wetlands consisting of ‘‘a mosaic of varying types of scenery from small and large rivers, ponds, swamps and floodplains to wooded areas which remain dry all year long’’ (Dubs, 1992: 433). Unfortunately, we have no record of the specific habitat in which the three rats were captured. In their survey of the Pantanal, Alho et al. (1987) obtained samples of *Oligoryzomys*, *Oecomys*, and *Oryzomys subflavus*, but no *O. nitidus*.

Paraguay and Argentina: The two examples from eastern Paraguay and single specimen from northeastern Argentina are from currently or formerly forested areas representing southern extensions of the tropical and subtropical Atlantic Forest formation (see map in Hueck and Seibert, 1981; Myers, 1982, discussed eastern Paraguayan habitats). Of the two specimens reported by Massoia (1974: 2), for example, the trapping habitat for one was a ‘‘place inside the subtropical eastern forest, possessing intricate vegetation and with a landscape in general very little modified by human presence.’’ The other specimen was caught at a locality in which the habitat was ‘‘similar to the preceding but on the edge of a trail.’’ (Both quotes were translated from the Spanish by E. Brothers.)

SYMPATRY

The distribution of collection records for *O. nitidus* overlaps the geographic distributions of four other species included in the former *O.* ‘‘*capito*’’ complex (specimens are identified in appendices B and G; also compare localities for *O. megacephalus* in table 1 with those in gazetteer for *O. nitidus*). Either *O. megacephalus* or *O. yunganus* or both have been trapped along with *O. nitidus* in Perú (localities 57, 58, 60, and 63 in gazetteer for *O. nitidus*), adjacent Amazonian Brazil (locality 141), and Bolivia (localities 72–76, 90, 127, 128, 130, and 134). On the fringe of southeastern Amazonia in the Serra do Roncador (locality 142), one example of *O. nitidus* was captured along with large series of *O. megacephalus* and *O. yunganus* in gallery forest (capture data from field journal of I. Bishop, in archives of the British Museum; also see appendix G).

Geographic ranges of *O. nitidus* and *O. macconnelli* overlap extensively in Peruvian Amazonia, but our documented records based on specimens studied indicate that the two species have been collected together only at Balta (locality 60 in gazetteer for *O. nitidus*). There, a single example of *O. macconnelli* was trapped in a narrow band of primary forest along a stream bordered otherwise by second-growth forest (see habitat section in account of *O. macconnelli*), and large series of *O. nitidus* were collected in young second-growth forest that was once a garden (see habitat account above for Peruvian *O. nitidus*; specimens are identified in appendix G).

Other records of co-occurrence, based only on sightings or specimens we have not examined, are from Departamento Madre de Dios in southeastern Perú. Pacheco et al. (1993) reported *O. nitidus* and *O. macconnelli* from the Cocha Cashu Biological Station at about 380 m on the left bank of the Río Manu in the Manu Biosphere Reserve (also see Voss and Emmons, 1996: 108); this record is not represented by voucher specimens. Pacheco (personal commun.) also told us that he trapped both species at Pakitza, which is a guard station at about 360 m ‘‘located just outside Parque National Manu, about 21 km ESE of Cocha Cashu and on the same (left) bank of the Río Manu’’ (Voss and Emmons, 1996: 106); this material is housed at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos in Lima.

The documented range of *O. nitidus* is allopatric to the other species in the group (fig. 79). No records approach the distribution of the sample from Pará (localities 148–150 in gazetteer). The ranges of *O. nitidus* and *O. russatus* are also largely exclusive of each other except in southern Bolivia, where both species have been collected in the state of Santa Cruz near Estancia Las Cuevas (localities 140 and 151 in gazetteers for *O. nitidus* and *O. russatus*, respectively), a site in highly disturbed gallery forest. There, one *O. russatus* (MSB 67321) and an example of *O. nitidus* (MSB 70697) were trapped on May 25, 1991 ‘‘Along edge of soccer field in heavy undergrowth, 15′ canopy, shady, leaf litter, forbes, vines. Cover at shrub and ground 75%, canopy 80%.’’ Several *O. nitidus* were trapped in other places at Las Cuevas (see above in habitat section of Bolivian specimens).

DESCRIPTION OF THE SPECIES

Gardner and Patton (1976) captured the essence of the species. It is moderately large in body size with a tail equal to or conspicuously longer than length of head and body (table 37). Fur covering the entire upperparts is rich, tawny brown (russet), imperceptibly grading to buffy ochraceous highlights near the demarcation between upperparts and underparts. The coat is soft to the touch and short (5–8 mm). The ventral coat is lustrous whitish gray. Ears are dark brown, their inner and outer surfaces sparsely covered with short and fine tawny hairs. The longest mystacial vibrissae, when laid against the study skin, reach the posterior margin of the pinnae but do not extend beyond it. The tail is sparsely haired and bicolored; its dorsal surface is brown, and the ventral surface is unpigmented or lightly mottled for much of its length, with the distal one-half to one-fourth being either mottled, pale brown, or the same tone as the upper surface. Hind feet are long and narrow, with the plantar surfaces adorned with six pads. Lengths of digits relative to one another and to the metatarsus closely resemble the proportions shown for *O. yunganus* and *O. megacephalus* in figure 17. Dorsal surfaces of front and hind feet are densely covered by silvery white hairs so that the feet appear solid white (unless dis-

Fig. 80. Cranium and dentary of an adult *Oryzomys nitidus* (USNM 390065) from 4 km W Puerto Maldonado, Departamento de Madre de Dios, Perú. ×3.

colored by grease in dry museum specimens, in which case the feet appear tan). Each claw is nearly hidden by a thick sheath of silvery white hairs that extends well beyond the claw tip. Females have eight mammae (one pectoral pair, one postaxillary pair, one abdominal pair, and one inguinal pair).

Juveniles resemble the adults in overall

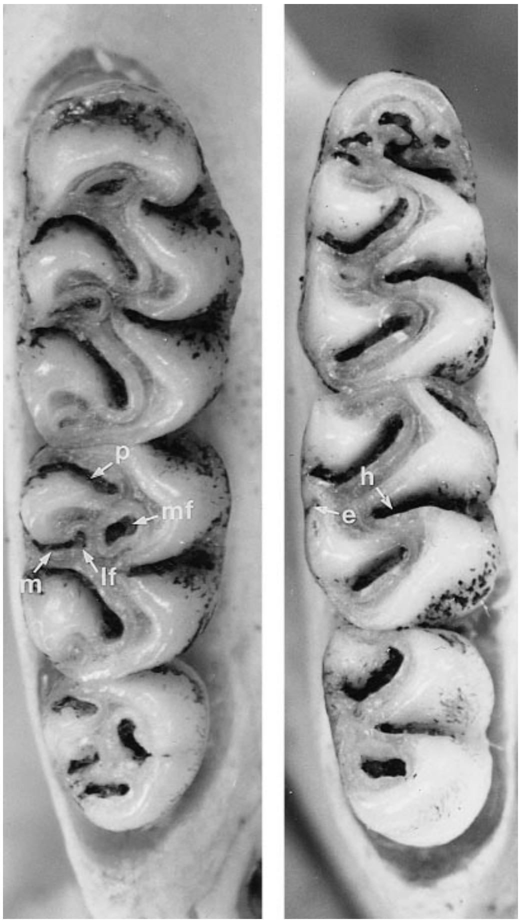

Fig. 81. Occlusal views of right upper and lower molar rows of *Oryzomys nitidus* as represented by MNFS 1309 from Igarapé Porongaba on the right bank of Rio Juruá, Estado do Amazonas, Brazil. In the upper second molar, note the short paraflexus (**p**), the medial fossette (**mf**), and the mesoflexus (**m**) with additional wear; the mesoflexus is isolated as a labial fossette (**lf**). The second lower molar has a short hypoflexid (**h**) and a creaselike entoflexid (**e**). See also figures 29–32.

coloration and tail pattern. Upperparts are appreciably duller, the dorsal surface brownish gray, and the sides of head and body are tawny buff. Underparts are also whitish gray, but dull because of the short hairs that form the coat, and contrast with the white sheen seen in the longer adult coat.

The cranium of *O. nitidus* is long and slender (fig. 80). Its overall shape is not unlike that of other species in the *O. nitidus* group (figs. 82, 83, 89, 90, 98, and 99). All group members share an elongated rostrum, moderately wide interorbit in which the dorsolateral margins are outlined by low ridges, an unremarkable braincase, small auditory bullae, and a primitive carotid circulatory pattern (including a sphenofrontal foramina, squamosoalisphenoid grooves, a large stapedial foramina, and a groove on the ventral surface of each pterygoid plate for the infraorbital branch of the stapedial artery). *Oryzomys nitidus* has elongate incisive foramina, a short bony palate, wide zygomatic plates, and correspondingly deep zygomatic notches. Approximately half the total specimens surveyed have alisphenoid struts (table 38).

Like all other species in the former *O.* ‘‘*capito*’’ complex, the upper incisors of *O. nitidus* are opisthodont in configuration relative to the rostral axis. The enamel of upper and lower incisors is yellow-orange or deep orange.

Molars are tuberculate and brachydont with two rows of cusps arranged in opposing labial–lingual pairs (fig. 81). Occlusal patterns of the cusps and folds are similar to the configurations found in all other species of the *O. nitidus* group and in *O. yunganus*. In contrast to the patterns exhibited by samples of *O. megacephalus*, *O. laticeps*, *O. bolivaris*, and *O. talamancae*, the second upper molars of *O. nitidus* and its allies have both a labial and a medial fossette (enamel island, as described by Gardner and Patton, 1976: 39), their second lower molars usually show a fossettid (see fig. 32 where a fossettid is present in the example of *O. nitidus*; the specimen shown in fig. 81 lacks a fossettid), and they always have a short hypoflexid extending only halfway across the molar that is counterpointed by a creaselike entoflexid (see figs. 30 and 32 where occlusal patterns are contrasted among *O. yunganus*, *O. macconnelli*, *O. nitidus*, and *O. megacephalus*).

Chromosomal characteristics of a few samples from Perú were documented by Gardner and Patton (1976). The diploid number is 80 and the fundamental number is 86 (table 13). This karyotype is identical to that reported for *O.* ‘‘*capito*’’ (= *O. russatus*) from Estado do São Paulo, Brazil, by Almeida (1980, fide Maia, 1990) and for ''*nitidus*'' [= *russatus*] by Silva (1994).

COMPARISONS WITH SOME SPECIES IN THE FORMER *ORYZOMYS* ''*CAPITO*'' COMPLEX

Oryzomys nitidus and its close relatives in the *O. nitidus* group are similar in fur coloration as well as in cranial and dental morphology. They are readily distinguished from other species in the former *O.* ''*capito*'' complex—*O. megacephalus*, *O. laticeps*, *O. yunganus*, *O. bolivaris*, and *O. talamancae*; fig. 151, table 52). We have already contrasted *O. yunganus* with *O. nitidus* and *O. macconnelli* (see text and illustrations in account of *O. yunganus*). Compared with *O. nitidus* and its allies, *O. megacephalus* and *O. laticeps* have duller pelage than any member of the *O. nitidus* group, a different cranial configuration (see figs. 18–22), and a modified cephalic arterial pattern (no sphenofrontal foramina and squamosoalisphenoid grooves). Occlusal patterns of second upper molars are characterized by a long paraflexus and labial fossette, but have no medial fossette (enamel island); lower second molars have a long hypoflexid that nearly bisects the tooth (see figs. 29–32). Chromosomal traits also set *O. megacephalus* and *O. laticeps* apart from *O. nitidus* and its allies (table 13).

Although examples of *O. nitidus* in museum collections have been misidentified as either *O. yunganus* or *O. megacephalus*, we never found specimens of *O. nitidus* confused with the two trans-Andean species, *O. talamancae* and *O. bolivaris*. This is surprising because the cranial conformation exhibited by those two species is like that of *O. nitidus*. Furthermore, except for smaller body size, specimens of *O. talamancae* and *O. nitidus* are strikingly similar in fur coloration and texture, tail pattern, and general proportions of external dimensions (compare the descriptive statistics for external, cranial, and dental measurements of *O. talamancae* given in Musser and Williams, 1985: 15, with those for external measurements of *O. nitidus* in table 37 as well as the cranial and dental measurements listed in appendix E). Occlusal patterns of second upper and lower molars, however, are dissimilar. The patterns found in *O. talamancae* are like those typical of *O. megacephalus*, not of *O. nitidus* and its allies (see text and figures in the account of *O. talamancae* as well as fig. 151 and table 52). Molar occlusal patterns of *O. bolivaris* closely resemble those of *O. talamancae* (see account of the former). The long and dense fur of *O. bolivaris* as well as its exceptionally long facial vibrissae provide strong contrast to *O. nitidus* and the other members in its group. Finally, compared with *O. nitidus* and its relatives, both trans-Andean species are characterized by different chromosomal complements (table 13) and geographic distributions either exclusively west or northeast of the Andes (see the maps in figs. 50, 66, 78, and 79 for *O. bolivaris*, *O. talamancae*, *O. macconnelli*, and *O. nitidus* and its allies, respectively).

COMPARISONS WITH OTHER SPECIES IN THE *ORYZOMYS NITIDUS* GROUP

Discrete qualitative traits distinguish *O. nitidus* from the trans-Andean *O. bolivaris* and *O. talamancae*, the Amazonian *O. yunganus* and *O. megacephalus*, and the Atlantic Forest *O. laticeps*; however, no such comparable features will separate *O. nitidus* from other members in the *nitidus* group. All species in the *nitidus* group closely resemble one another in pelage coloration, tail pattern, cranial conformation, and molar occlusal patterns. In addition to geographic distributions, quantitative rather than qualitative features form the primary distinctions among the species, contrasts related to absolute and relative differences in dimensions. We begin by contrasting *O. nitidus* with *O. macconnelli* and the series of specimens from central Estado de Pará, Brazil (population sample 18 in table 39), which we will refer to as simply the Pará Sample. We formally name and describe this entity in an account following those of *O. nitidus* and *O. macconnelli*. The next set of comparisons involves *O. nitidus* and samples from southern Bolivia and northern Argentina that have previously been identified as *O. legatus* (for example, by Musser and Carleton, 1993). Finally, we document our reasons for including *legatus*, *lamia*, and *kelloggi*, all provisionally treated as species by Musser and Carleton (1993), within *O. rus-*

TABLE 37

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weights (g) from Selected Samples of Species in the *Oryzomys nitidus* and *Oryzomys subflavus* Groups

(Mean, ± 1 SD, observed range in parentheses, and size of sample are listed. The ratio LT/LHB was computed from mean values. Each sample contains the range in age from young to old adults. Number in parentheses refers to numbered collection locality in gazetteer. Specimens measured are identified in footnotes. See table 49 for measurements of types.)

Species and sample	LHB	LT	LHF	LE	W	LT/LHB (%)
Oryzomys macconnelli						
VENEZUELA[a]						
(11)	140.3 ± 0.77 (119–153) 7	154.7 ± 16.15 (135–178) 7	36.9 ± 1.62 (35–37) 7	24.6 ± 1.62 (22–26) 7	89.3 ± 17.89 (65–115) 7	110
(13)	144.9 ± 12.27 (132–166) 12	160.1 ± 9.56 (143–175) 12	34.2 ± 1.59 (32–37) 12	—	—	111
ECUADOR + PERÚ[b]						
(23 + 26)	149.1 ± 12.69 (134–172) 11	140.7 ± 9.99 (127–159) 11	34.3 ± 1.27 (32–36) 11	—	—	94
PERÚ[c]						
(25)	148.3 ± 1.71 (146–150) 4	142.8 ± 5.91 (135–149) 4	34.8 ± 0.96 (33–36) 4	25.5 ± 1.00 (25–27) 4	83.6 ± 2.39 (81.5–87.0) 4	96
(40)	145.9 ± 10.46 (130–160) 7	138.6 ± 11.86 (124–157) 11	34.7 ± 1.00 (33–37) 11	22.0 ± 1.00 (21–23) 7	—	95
BRAZIL[d]						
(43 + 44)	144.7 ± 4.11 (135–150) 10	150.5 ± 9.86 (130–160) 10	34.8 ± 1.14 (33–36) 10	23.5 ± 1.08 (22–25) 10	87.4 ± 9.13 (73–105) 10	104
(47–49)	126.4 ± 9.72 (110–145) 20	135.2 ± 12.87 (115–160) 20	33.6 ± 1.50 (30–60) 10	22.7 ± 1.03 (21–24) 6	70.6 ± 17.76 (50–110) 20	107
(50)	137.8 ± 6.26 (130–146) 5	147.2 ± 13.81 (131–167) 5	34.8 ± 1.10 (33–36) 5	21.2 ± 1.30 (20–23) 5	65.7 ± 9.79 (49.5–73.8) 5	107
(55)	134.9 ± 7.62 (125–155) 17	145.1 ± 10.59 (130–165) 17	34.4 ± 1.37 (32–37) 17	—	74.3 ± 13.86 (55–106) 16	108
Oryzomys nitidus						
PERÚ[e]						
(60)	136.8 ± 7.27 (121–148) 18	126.8 ± 10.03 (108–147) 17	32.6 ± 1.38 (31–36) 18	21.4 ± 1.00 (19–23) 12	74.6 ± 13.75 (55–99) 12	93
(69)	139.9 ± 9.14 (121–163) 31	132.3 ± 9.44 (116–154) 31	32.0 ± 1.80 (27–36) 31	21.0 ± 1.49 (17–24) 31	73.9 ± 13.71 (49–103) 31	95
BOLIVIA[f]						
(86)	131.9 ± 9.24 (115–147) 42	140.6 ± 11.24 (121–168) 42	33.0 ± 1.35 (31–35) 42	23.5 ± 1.44 (20–27) 42	61.0 ± 12.34 (41–86) 42	107
(131 + 132)	132.2 ± 7.85 (119–149) 21	138.7 ± 8.76 (112–151) 21	32.0 ± 1.61 (30–35) 21	23.2 ± 1.22 (22–26) 21	67.4 ± 12.53 (50–90) 21	105
BRAZIL						
(141)[g]	139.3 ± 11.90 (126–149) 3	139.0 ± 9.54 (133–150) 3	34.3 ± 1.53 (33–36) 3	22.7 ± 0.58 (22–23) 3	76.3 ± 14.57 (60–88) 3	100
PARAGUAY[h]	149	152	33	26	90	102
ARGENTINA[i]	119	130	33	22	—	109
Pará Sample						
BRAZIL[j]						
(148)	133.7 ± 7.37 (128–142) 3	152.0 ± 11.31 (144–160) 2	34.3 ± 0.58 (34–35) 3	23.3 ± 0.58 (23–24) 3	72.0 ± 7.21 (64–78) 3	114

TABLE 37
(*Continued*)

Species and sample	LHB	LT	LHF	LE	W	LT/LHB (%)
(149)	128.0 ± 6.75 (120–140) 10	145.0 ± 10.00 (130–160) 10	33.2 ± 1.03 (32–35) 10	—	56.3 ± 6.11 (46–66) 10	113
Oryzomys russatus						
BOLIVIA[k]						
(154 + 156)	135.9 ± 9.87 (124–158) 10	141.5 ± 6.04 (134–152) 10	33.5 ± 1.43 (31–35) 10	25.0 ± 0.67 (24–26) 10	65.2 ± 12.67 (50–94) 10	104
ARGENTINA[l]						
(165–167)	125.4 ± 10.17 (110–142) 8	152.6 ± 7.52 (140–165) 8	33.9 ± 0.99 (33–35) 8	— (43–88) 8	62.0 ± 17.55	122
BRAZIL[m]						
(184)	141.8 ± 6.21 (128–153) 25	153.3 ± 8.57 (140–175) 25	34.4 ± 1.35 (32–37) 25	23.3 ± 1.31 (20–26) 25	—	108
(195 + 196)	143.7 ± 15.07 (120–160) 9	145.6 ± 7.30 (134–160) 9	34.7 ± 1.50 (32–37) 9	— (60–110) 9	83.7 ± 17.51	101
(199)	140.0 ± 5.00 (135–145) 5	144.2 ± 6.94 (138–153) 5	34.8 ± 0.84 (34–36) 5	23.6 ± 0.89 (22–24) 5	—	103
(200)	152.5 ± 4.63 (145–160) 8	153.1 ± 6.51 (145–165) 8	35.1 ± 1.13 (33–37) 8	24.0 ± 0.54 (23–25) 8	91.4 ± 10.69 (70–100) 7	100
Oryzomys subflavus						
BRAZIL[n]	162.9 ± 14.40 (145–200) 12	192.5 ± 16.58 (170–220) 12	35.3 ± 1.36 (33–37) 12	20.8 ± 0.83 (19–22) 12	102.1 ± 27.09 (75–170) 12	118
BOLIVIA[o]	150.4 ± 8.68 (137–164) 12	182.8 ± 6.64 (175–198) 12	36.0 ± 0.43 (35–37) 12	20.8 ± 0.94 (19–22) 12	83.7 ± 16.38 (54–115) 11	122

[a] Same specimens that are listed for sample 2 in appendix F.

[b] BMNH 54.442, 54.444–54.447, 54.450, 54.451–54.453, 54.455, 54.459.

[c] **(25)**, RMT 4080, 4087; NW 879, 881. **(40)**, FMHN 75268, 75271, 75274, 75276–75279.

[d] **(43 + 44)**, JLP 15548, 15563, 15600, 15619, 15859; MNFS 529, 530, 550, 563, 747. **(47–49)**, USNM 461784, 521533–521535, 544606, 544607, 544609–544612, 544615–544623, 545293, 545294. **(50)**, USNM 519772–519774, 519776, 521437. **(55)**, USNM 394208, 394211, 394212, 394214–394216, 394218–394221, 394224–394227, 394229, 294230, 294232, 543355.

[e] **(60)**, LSUMZ 12333, 12335–12343, 14356, 14357, 14365, 16690; MVZ 136574, 136578, 136588. **(69)**, 144458–144460, 144465, 144466, 144468, 144470, 144471, 144474, 144475, 144477, 144480, 144481, 144484, 144487–144489, 144492, 144493, 144497, 144499, 144500, 144503–144505, 144508, 144510, 144511, 144513, 144516, 144517.

[f] **(86)**, AMNH 264733, 264734, 264738–264745, 264747, 264748, 264751–264755, 264757–264763, 164765, 264767; MSB 68451, 68454, 68456–68460, 68462–68464, 68466–68470, 68472. **(131 + 132)**, USNM 390072, 390073, 390076–390083, 390085, 390090–390092, 390094, 390098, 390100–390102, 390104, 390105.

[g] **(141)**, MNFS 1147, 1223, 1419.

[h] UMMZ 126008 (locality 146 in gazetteer for *O. nitidus*).

[i] BMNH 24.6.6.42 (locality 147 in gazetteer for *O. nitidus*).

[j] **(148)** MZUSP 27150; USNM 549551, 549552. **(149)**, 543327–543329, 543331, 543332, 543334–543338.

[k] **(153 + 155)**, AMNH 263881–263887; MSB 63359, 63360, 63584.

[l] **(165–167)**, CM 43821–43827, 72391.

[m] **(184)**, USNM 461989, 484027–484038, 484040–484042, 485001, 485002, 485005, 485006, 485011, 485014–485016, 485020. **(195 + 196)**, USNM 304562–304569, 332452. **(199)**, BMNH 1.11.3.29, 1.11.3.30, 1.11.3.32–1.11.3.34. **(200)**, AMNH 134644, 134663–134667, 134677, 134772.

[n] Goiás: AMNH 134518, 134629, 134633, 134636, 134645, 134648, 134674, 134675. Mato Grosso: AMNH 134705, 134708, 134710, 134712.

[o] Santa Cruz: AMNH 246934, 260378, 260380, 260381, 260383–260388, 263342, 263343.

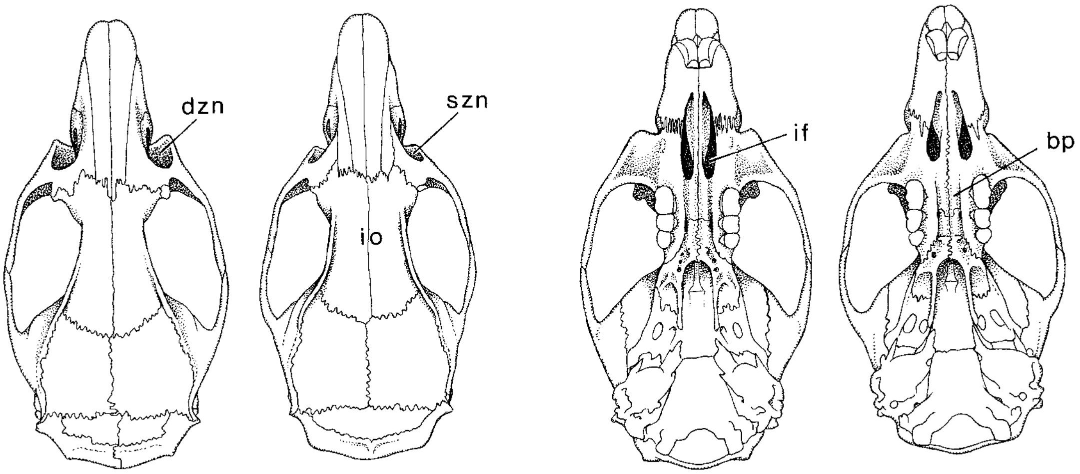

Fig. 82. Dorsal (**left pair**) and ventral (**right pair**) views of crania illustrating qualitative contrasts between adult *Oryzomys* from along the Rio Juruá, Brazil. Left member of each pair: *O. nitidus* (MNFS 1223) from Igarapé Porongaba, right bank, Estado do Acre (locality 142 in gazetteer of *O. nitidus*). Right member of each pair**:** *O. macconnelli* (JLP 15563) from Seringal Condor, left bank, Estado do Amazonas (locality 44 in gazetteer for *O. macconnelli*). The interorbit (**io**) is narrow in *O. nitidus*, the zygomatic notch is deep (**dzn**), the incisive foramina (**if**) are long and narrow, and the bony palate (**bp**) is short. In contrast, the interorbit is wider in *O. macconnelli*, the zygomatic notch is shallow (**szn**, reflecting a narrower zygomatic plate; see fig. 83 on opposite page), incisive foramina are short and diverge posteriorly, and the bony palate is long (a function of the shorter incisive foramina). These differences between the two species are also reflected in the ratio diagram (fig. 84).

satus, and compare that species with *O. nitidus*.

Oryzomys nitidus, *Oryzomys macconnelli*, and the Pará Species

Researchers working with samples from the Guiana Region, where *O. nitidus* does not occur, have had no difficulty identifying *O. macconnelli* (Tate, 1939; Pine, 1973; Husson, 1978). Where the ranges of these two species do overlap in Perú, Gardner and Patton (1976) were able to identify specimens captured at Balta as either *O. nitidus* or *O. macconnelli* by using differences in pelage color and texture as well as chromosomal complements as their primary discriminators. To appreciate and test the differences between the two species, we first studied samples of *O. macconnelli* from the Guiana Region (including the type series from Guyana) and compared these samples with the type series of *O. nitidus* and other samples from Perú, especially those collected at Balta. We discovered that the chromatic and morphological distinctions between the two were not always so clear in every pair of samples, even in some from Perú. We initially misidentified certain samples as either one or the other species, and only after we had tested our sorting with morphometric analyses were we satisfied with our revised determinations. The series from central Pará (the Pará Sample, localities 148–150 in gazetteer for *O. nitidus* group) was especially intractable to identification. In our initial sorting of skins and skulls, we identified the specimens as *O. macconnelli*, even though they did not quite fit with that species. A preliminary qualitative analysis suggested that the Pará specimens do not represent *O. macconnelli*. We also discovered that examples of the Pará series and *O. macconnelli* had been collected together at one place (locality 50 in gazetteer for *O. macconnelli*). Some characteristics of the Pará material seem to fit those we associated with *O. nitidus*, and in the morphometric analyses we initially treated the Pará Sample as eastern Amazonian Basin repre-

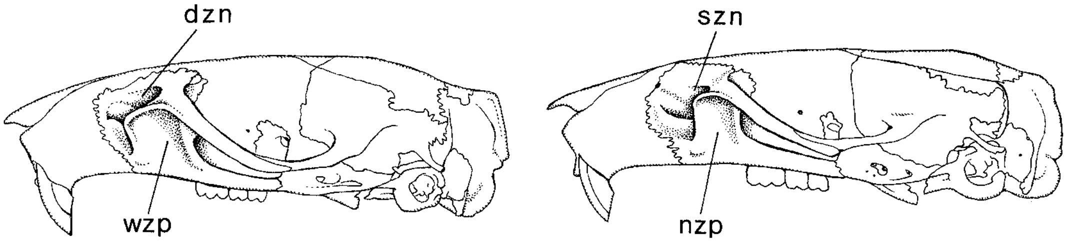

Fig. 83. Lateral views of same crania of *Oryzomys* (illustrated in fig. 82 on opposite page) showing differences in zygomatic plate. **Left:** *O. nitidus*. **Right:** *O. macconnelli*. The plate is much wider in *O. nitidus* both in absolute values (see sample means of each species listed in appendix E) and relative to other cranial dimensions (see ratio diagram in fig. 84). The broader plate (**wzp**) reflects the greater anterior projection of the free margin and results in a deeper zygomatic notch (**dzn**) of the maxillary in contrast to the narrower plate (**nzp**) and shallower notch (**szn**) observed in specimens of *O. macconnelli*.

sentatives of *O. nitidus*. Subsequent study, however, demonstrated that specimens in the Pará Sample were distinct even from *O. nitidus*.

In external appearance, samples of *O. nitidus*, *O. macconnelli*, and the Pará series closely resemble one another. Most examples of *O. macconnelli* have darker fur (which imparts a richer sheen to the dorsal appearance) covering the upperparts of head and body that is appreciably longer (11–15 mm in 17 adults from Auyán Tepuy, for example) and feels softer (‘‘long and lax,’’ in the words of Gardner and Patton, 1976: 40). The pelage is dark reddish brown in *O. macconnelli* as opposed to bright tawny brown (with more yellowish tones) in most *O. nitidus*, but the overlap in color variation between the two species is considerable, rendering this trait less useful in separating the species. Even Gardner and Patton (1976), for example, described the pelage of both *O. nitidus* and *O. macconnelli* as ‘‘reddish brown.’’

Individuals in the Pará Sample closely resemble specimens of *O. nitidus* in coloration, but they are also chromatically similar to some examples of *O. macconnelli* collected in the same geographic region. Specimens from Pará contrast with most specimens of *O. macconnelli* by their shorter dorsal fur that forms a bright tawny brown coat with more yellowish buff than reddish tones; this distinction is best appreciated in specimens having prime adult coats. The tail averages longer relative to the head and body in members of the Pará Sample than in series of either *O. macconnelli* or *O. nitidus* (table 37).

Overall size is similar in *O. nitidus* and *O. macconnelli*, as suggested by their close mean values (table 37) for many external, cranial, and dental variables (appendix E). But means for measurements of certain cranial variables are not so close and this absolute average size difference can be detected by examining crania of the two species side-by-side, providing they represent individuals of roughly similar age as judged by degree of molar wear. These contrasts are clearly illustrated in figures 82 and 83. Compared with specimens of *O. macconnelli*, examples of *O. nitidus* have a narrower interorbit, much wider and more robust zygomatic plate with a correspondingly deeper zygomatic notch, longer and narrower incisive foramina, and shorter bony palate.

These visual distinctions are also revealed as proportional differences in the ratio diagram (fig. 84) in which we compare a large sample of *O. nitidus* from Perú with a substantial series of *O. macconnelli* from Ecuador and Perú. It is clear from the diagram that, relative to occipitonasal length and many other cranial dimensions, *O. macconnelli* has a significantly wider interorbit, narrower zygomatic plate, longer bony palate, and shorter and much wider incisive foramina than does *O. nitidus*.

We noted another proportional difference in the skulls of the two species, although it is less conspicuous than those described above. Specimens of *O. nitidus* tend to have a narrower, less inflated rostrum than do examples of *O. macconnelli*. Mean values of rostral breadth in most samples of *O. nitidus*

TABLE 38
Frequency of Occurrence of Alisphenoid Struts in Samples of the *Oryzomys nitidus* Group[a]

Species and country (numbers key to localities in gazetteer for *O. nitidus* group)	Number of specimens with (+) or without (–) alisphenoid struts on left and right side of braincase			
	+ +	+ –	– +	– –
O. nitidus				
PERÚ (56, 57, 59, 60, 62, 67, 68)	22	—	1	15
BRAZIL (141, 143, 144)	4	2	—	1
BOLIVIA (70–76, 79, 80, 82, 83, 85–90, 94, 95, 97, 98, 100–103, 105, 108, 112, 113, 116, 118, 122,127, 128, 130–140)	89	14	13	54
PARAGUAY (145, 146)	—	—	—	2
O. macconnelli				
FRENCH GUIANA (1), SURINAM (4, 7), GUYANA (9, 10), VENEZUELA (11–14), ECUADOR (18, 19)	—	—	—	45
PERÚ (24, 29, 33, 36, 37)	—	—	1	16
BRAZIL (43, 44, 46–50, 52–55)	—	—	1	82
Pará Sample				
BRAZIL (148–150)	1	—	—	14
O. russatus				
BOLIVIA (152–160, 162, 163)	21	1	—	—
ARGENTINA (168, 169)	4	1	—	—
BRAZIL (172, 173, 176, 181, 183–188, 194–198, 199–201)	28	10	5	43

[a] On each side of the braincase, the bony alisphenoid strut separates masticatory-buccinator foramina from the foramen ovale accessorius; these foramina are confluent in specimens lacking the strut (see illustrations in Carleton and Musser, 1989: 36, and Voss, 1991: 28). The strut varies in thickness among specimens of the *O. nitidus* group, ranging from a thick pillar to a thread of bone; all expressions of the strut within this range were coded as present. We did not discriminate partial or incomplete struts but coded them as absent; very few specimens exhibited such a borderline morphology. Struts are usually present on both sides of the braincase but in some specimens may be present on one side and absent from the other, a variation we also tabulated.

are slightly smaller than those for most *O. macconnelli*, but the difference is not appreciable (see appendix E). However, our perception is reinforced by the ratio diagram (fig. 84) where the sample of *O. macconnelli* is indicated to have a wider rostrum relative to its length compared with *O. nitidus*.

A qualitative contrast also helps to distinguish between the two species. Alisphenoid struts are present in about half of all the specimens of *O. nitidus* we examined, but are absent from all but two examples of the *O. macconnelli* surveyed, and in these two a thin strut was present on only one side of the skull (table 38).

In summary, specimens in hand can be qualitatively distinguished as either *O. nitidus* or *O. macconnelli* by observing the differences in dorsal pelage texture (and usually coloration and length), size and proportions of certain cranial variables, and frequency of occurrence of alisphenoid struts.

We tested the observations described above by subjecting the data from cranial and dental measurements to multivariate analyses. Localities and specimens were pooled

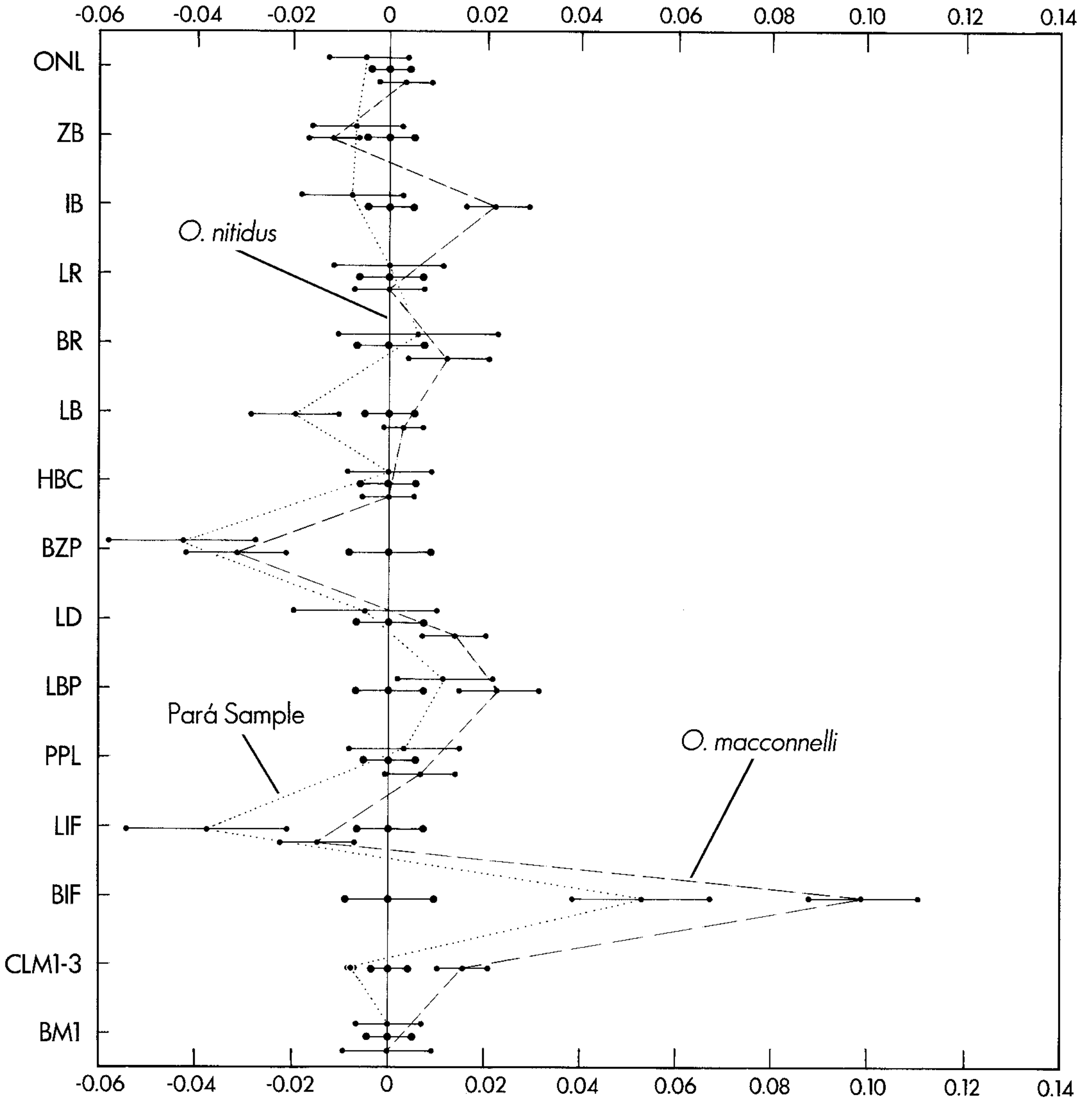

Fig. 84. Ratio diagram illustrating certain proportional relationships between population samples of adult *Oryzomys nitidus* from Departamento de Madre de Dios, Perú (the standard, sample 10, *N* = 42), *O. macconnelli* from Ecuador and Perú (sample 3, *N* = 32), and the Pará Sample from central Pará, Brazil (sample 18, *N* = 14). Data are derived from values for means, standard deviations, and sample sizes listed in appendix E. Localities constituting each population sample are indicated in table 39. Ratio diagrams are explained in Materials and Methods.

into population samples (or operational taxonomic units; localities constituting each sample, along with sample size, are listed in table 39; descriptive statistics for each sample are recorded in appendix E; and specimens measured and included in each of the samples are identified in appendix F). Certain cranial proportional differences are consistently revealed in principal components and canonical variate analyses, with contrasts reinforcing results of our visual examination of crania.

Results of principal components analysis comparing "typical" *O. nitidus* and *O. macconnelli*, based on specimens from the geographic regions of their respective type lo-

TABLE 39

Population Samples of the *Oryzomys nitidus* Group Used in the Multivariate Analyses

(Descriptive statistics for each sample are used in appendix E; specimens measured are listed in appendix F. Boldface number in parentheses indicates total number of specimens measured for each species. Total N = 502.)

Sample	N	Locality (number and name key to localities in gazetteer for the *O. nitidus* Group)	
Oryzomys macconnelli	**(151)**		
1. GUIANAS: French Guiana + Surinam + Guyana	17	1.	Arataye
		2.	Saül
		3.	Saint-Eugène
		4.	Brownsberg Nature Park
		7.	Rudi Kappelvliegveld
		8.	Bonasika River
		9.	Supenaam River
2. VENEZUELA: Bolívar	19	11.	San Ignacio de Yuruaní
		13.	Auyán-tepuí
3. ECUADOR: Pastaza + PERÚ: Loreto	32	23.	Río Tigre
		24.	Boca del Río Curaray
		25.	Teniente López
		26.	Huachi
4. PERÚ: Cuzco	10	37.	Río San Miguel
		38.	Cadena
		40.	Quincemil
5. BRAZIL: Amazonas	12	43.	Seringal Condor
		44.	Barro Vermelho
6. BRAZIL: W Pará	20	47.	Itaituba-Jacaréacanga
		48.	S Santarém
		49.	Altamira, 150 mi W
7. BRAZIL: E Pará	20	50.	Marabá, Perto Jatobal
		51.	Belém, Utinga
		52.	Capim
8. BRAZIL: Amapá	21	55.	Serra do Navio
Oryzomys nitidus	**(234)**		
9. PERÚ, Ucayali + Junín	22	60.	Balta
		63.	Amable María
10. PERÚ: Madre de Dios	42	68.	Puerto Maldonado
		69.	Cuzco Amazónica
11. BOLIVIA: Pando	11	70.	Río Nareuda
		71.	Bella Vista
		72.	La Cruz
		73.	Independencia
		74.	Palmira
		75.	Santa Rosa
		76.	Isla Gargantua
12. BOLIVIA: La Paz	48	86.	La Reserva
13. BOLIVIA: Beni	17	95.	N Yacuma
		96.	NW Yucumo
		98.	El Trapiche
		100.	San Ignacio

TABLE 39
(*Continued*)

Sample	*N*	Locality (number and name key to localities in gazetteer for the *O. nitidus* Group)
13. BOLIVIA: Beni (*continued*)		101. NNE San Ignacio
		102. W Casarabe
		103. Casarabe
		105. Río Mamoré
14. BOLIVIA: Santa Cruz-1	26	111. W Ascención
		112. Río Chaparé
		113. Río Ichilo
		116. Cachuela Esperanza
15. BOLIVIA: Santa Cruz-2	21	127. San Rafael de Amboró
		128. Río Saguayo
		130. Río Pitasama
16. BOLIVIA: Santa Cruz-3	21	131. La Abra
		132. Warnes
17. BOLIVIA: Santa Cruz-4	26	134. SW Las Cruces
		136. SE Santa Cruz
		137. Estación Pailón
		140. Estancia Las Cuevas
Pará Sample	**(14)**	
18. BRAZIL: Pará	14	148. Rio Xingu
		149. Marabá
		150. Marabá, Perto Jatobal
Oryzomys russatus	**(103)**	
19. BOLIVIA: Chuquisaca	15	152. Tola Orko
		153. Montecantu
		154. Río Limón
		157. E Chuhuayaco
20. BOLIVIA: Tarija	11	157. S Camatindi
		158. Caraparí
		159. WNW Caraparí
		160. WNW Entre Ríos
		161. Tapecua
		162. N Cuyambuyo
21. ARGENTINA: Salta + Jujuy	14	166. Piquirenda
		167. NW Agua Blanca
		168. E El Palmar
		169. E El Palmar
		170. El Simbolar
22. BRAZIL: São Paulo	38	184. Casa Grande
		185. Rio Guaratuba
23. BRAZIL: Espírito Santo + Minas Gerais	12	193. Nova Lombardia
		195. Além Paraíba
		196. Volta Grande
24. BRAZIL: Minas Gerais + Goiás	13	199. Ribeirão Jordão
		200. Anápolis

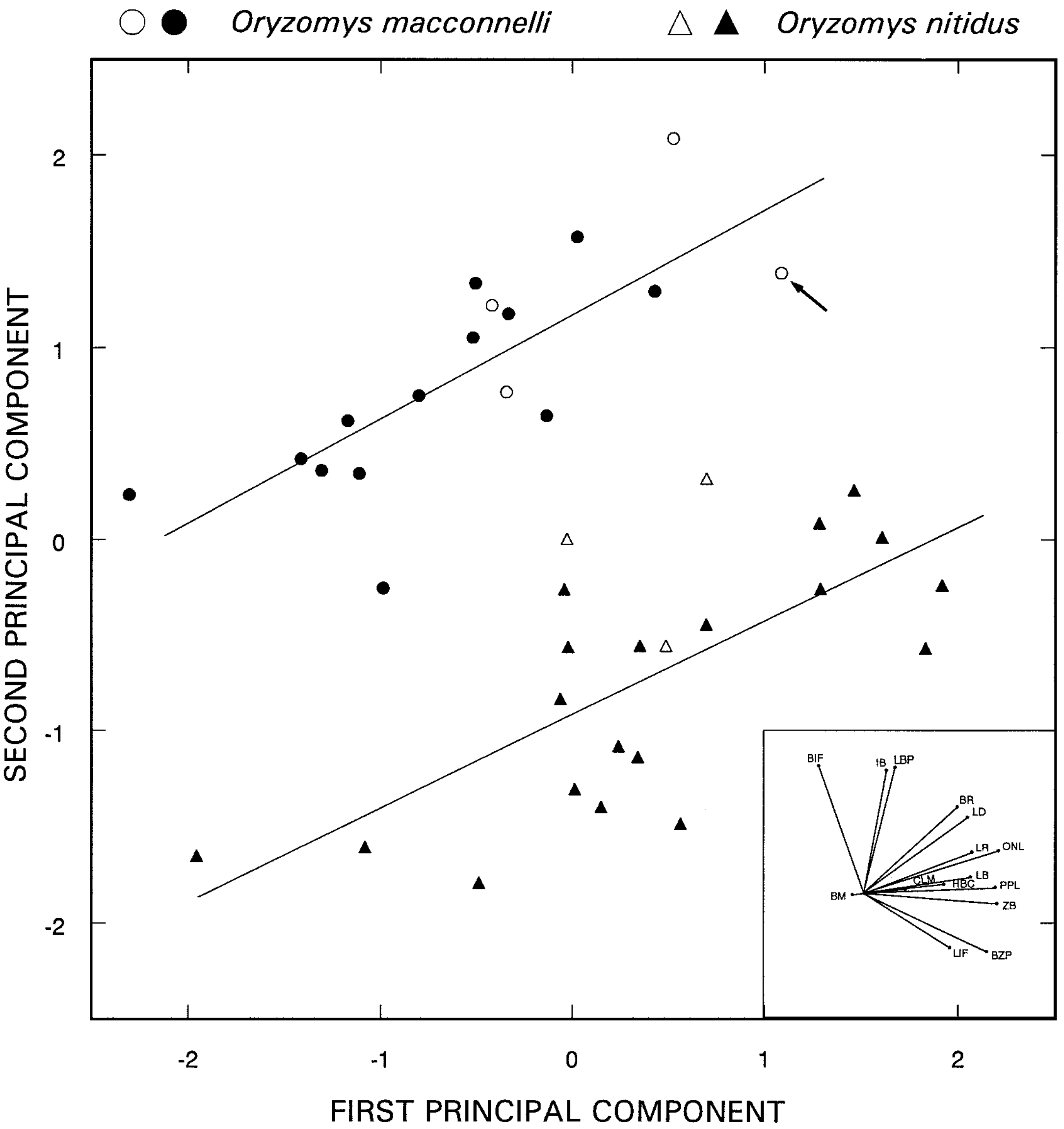

Fig. 85. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables and projected onto the first and second principal components extracted from analysis of adults from the region of the type localities of *Oryzomys macconnelli* (French Guiana, Surinam, and Guyana; sample 1, $N = 17$) and *O. nitidus* (central Perú; sample 9, $N = 22$). Open symbols identify specimens from the specific type localities of each species, including the holotype of *O. macconnelli* (indicated by arrow); three original topotypes of *O. nitidus* from Amable María are included, but not the damaged cranium of the holotype. Major axes of each constellation differ significantly in their Y-intercepts (1.18 versus -0.88, $P < 0.001$) but not in their slopes (0.55 versus 0.47, $P = 0.684$). **Inset:** Vectors of the cranial and dental variables corresponding to the magnitude and direction of their loadings (see table 40).

TABLE 40

Results of Principal Components Analysis of Specimens from the Region of the Type Localities of *Oryzomys macconnelli* (French Guiana, Surinam, Guyana; Sample 1) and *Oryzomys nitidus* (Central Perú; Sample 9)

(Localities constituting population samples 1 and 9 are listed in table 39, mean values for measurements of variables in each sample are listed in appendix E, and specimens measured are identified in appendix F. See fig. 85.)

	Principal components	
Variable	First	Second
ONL	0.91	0.29
ZB	0.90	−0.07
IB	0.15	**0.83**
LR	0.73	0.28
BR	0.63	**0.59**
LB	0.72	0.11
HBC	0.54	0.06
BZP	0.83	**−0.40**
LD	0.70	**0.52**
LBP	0.21	**0.86**
PPL	0.89	0.04
LIF	0.58	−0.37
BIF	−0.31	**0.87**
CLM1–3	0.28	0.03
BM1	−0.08	−0.01
Eigenvalue	0.024	0.021
% Variance	380.2	330.3

calities, are presented in figure 85 and table 40. If morphometrically pure *O. nitidus* or *O. macconnelli* exist, these representatives qualify and serve not only as a basis for explaining contrasts but as a test of our identifications from inspecting skulls. The holotype of *O. macconnelli* is included, along with three specimens of *O. nitidus* from the original type series (the holotype is excluded because the cranium is incomplete [see fig. 131], making it impossible to obtain a full set of measurements). Dispersion of scores along the first principal component reflects the lack of distinction in size of most cranial variables between specimens of each kind. There is, however, clear separation of the specimen scores along the second axis, primarily influenced by variation in breadths of interorbit and zygomatic plate, length of bony palate, and length and breadth of incisive foramina. Variation in breadth of rostrum and length of diastema also contributes to the dispersion of scores, although not as strongly (fig. 85 inset, table 40).

Discriminant function analyses of many more specimens, arranged in 18 population samples and covering a broader geographic area, reinforce the cranial distinctiveness of the two species *O. nitidus* and *O. macconnelli*. Separate clouds of specimen scores are clearly evident in the projection onto the first two canonical variates extracted (figs. 86, 87). Again, length of bony palate, breadth of zygomatic plate, and length and breadth of incisive foramina are the most decisive variables accounting for this hiatus between individual specimen scores and group centroids representing each species (fig. 87 inset, table 41). The wider interorbit of *O. macconnelli* and its somewhat broader rostrum and slightly longer diastema contribute less to the discrimination between the samples covering a broad geographic region; this outcome contrasts with their power of discrimination as disclosed in the principal components analysis where only specimens from the respective type regions were considered (fig. 85, table 40) and in the ratio diagram (fig. 84). Variation in length of molar row also contributes appreciably to interspecific discrimination along the first canonical variate, although it did not in the principal components analysis; molar rows of *O. macconnelli* do average longer than those of *O. nitidus* (see appendix E).

The multivariate analyses, combined with our initial observations and the record of sympatry at Balta, Perú, support the conclusion that most specimens segregate into two species. Each can be distinguished by absolute and proportional differences in certain cranial variables, and in most cases by dorsal pelage color and texture. (Note that the discriminant function analysis, from which the first and second canonical variates were extracted, is based on a priori definition of 18 groups [18 population samples in table 39], not two species; the latter is our deduction and is supported by the program's inability to segregate 18 kinds of rats in multivariate space.)

Some specimens included in the analyses, however, do not fit neatly with either *O. nitidus* or *O. macconnelli*. There is some overlap between the principal clouds of specimen

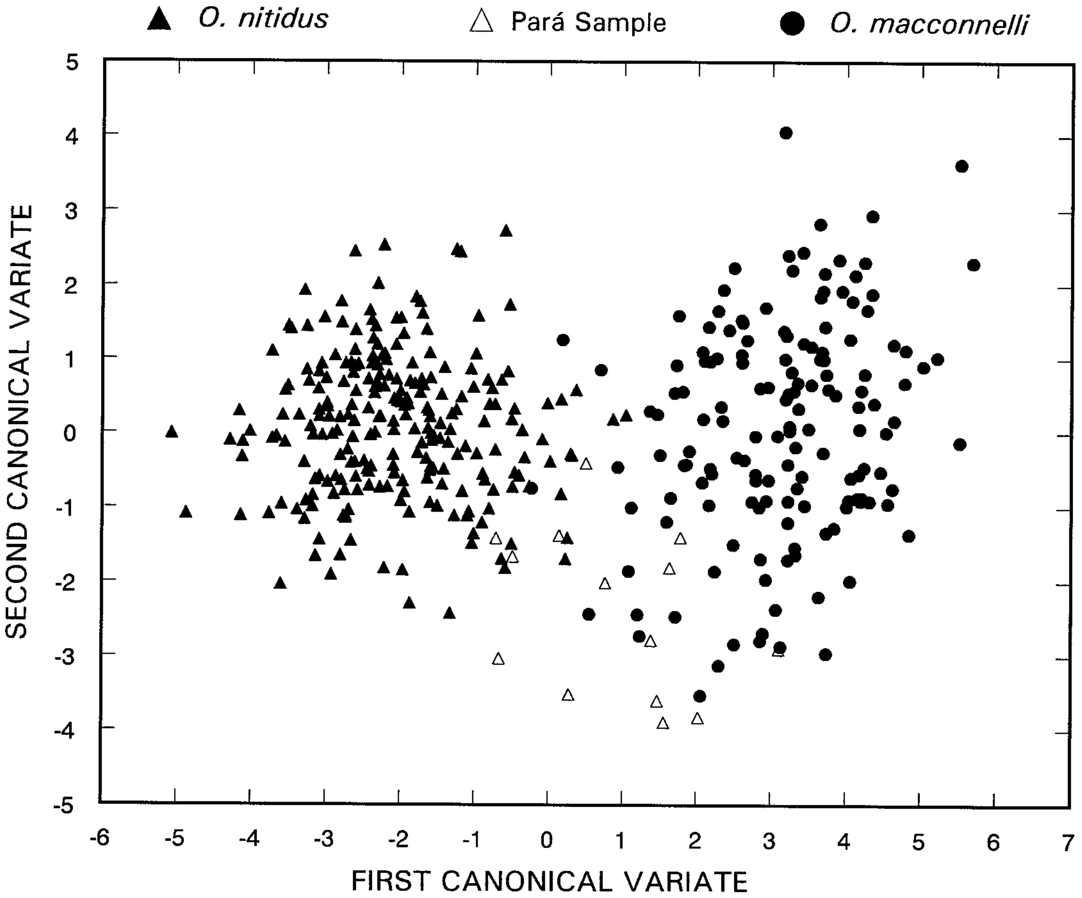

Fig. 86. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 41) and projected onto the first and second canonical variates derived from discriminant function analysis of 18 population samples representing *Oryzomys macconnelli* (samples 1–8, *N* = 151), *O. nitidus* (samples 9–17, *N* = 234), and the specimens from central Pará, Brazil (sample 18, *N* = 14). See also figure 87 on opposite page.

scores (fig. 86) that involves the series from Pará, population sample 18. Although we had viewed these specimens as *O. nitidus* in the discriminant function analysis, they were as much interspersed with scores representing *O. macconnelli*. This is reflected by the sample 18 centroid, which is isolated from the tight spacing of samples representing *O. nitidus* and is closer to those of *O. macconnelli* (fig. 87).

The enigmatic position of the Pará series is corroborated by clustering analyses (fig. 88). Weak association of this sample with *O. nitidus* is suggested by cranial and dental resemblance based on Mahalanobis' distances (the generalized distance between centroids over all 14 canonical variates that were derived, thus providing more information on canonical variates 3–14 that marginally linked sample 18 with *O. nitidus* than is visible in the scatter of the first and second canonical variates alone). However, measures of phenetic similarity, as indicated by Euclidean distances among population samples by using log-transformed means, portray the Pará series as close to a sample of typical *O. macconnelli* from western Estado de Pará (fig. 88). In either phenogram, samples of *O. nitidus* proper from along the eastern front of the Andes and adjacent lowlands are shown to be highly similar. So, what is the relationship of the Pará Sample?

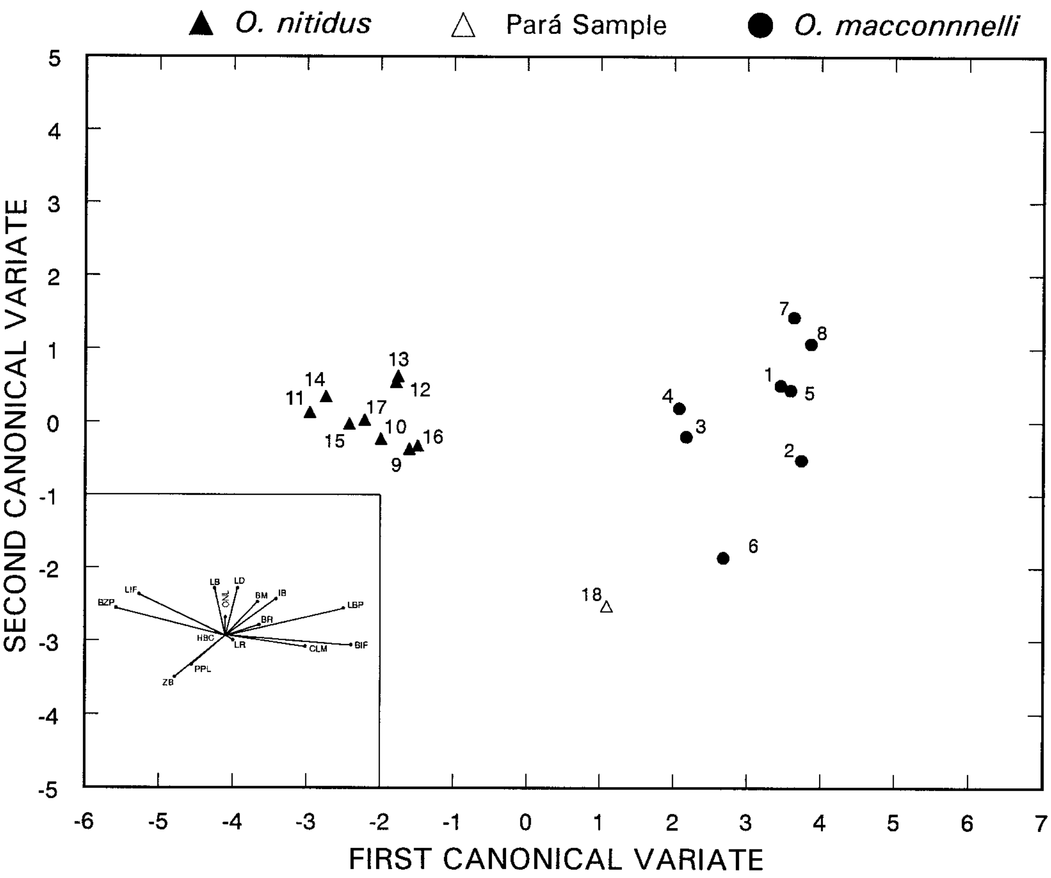

Fig. 87. Plot of group centroids on first two canonical variates derived from discriminant function analysis of 18 samples representing *Oryzomys macconnelli* (samples 1–8), *O. nitidus* (samples 9–17), and the series from Estado de Pará, Brazil (sample 18). See also figure 86 on opposite page. **Inset:** Vectors of 15 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (see table 41). Size of samples and the localities that constitute each sample listed in table 39.

In our initial sorting, we originally assigned the material from Pará to *O. macconnelli,* but realized our mistake after studying results of the multivariate analyses and looking again at the Brazilian samples. External traits of all specimens are similar, but those from certain localities in Pará have shorter and brighter dorsal pelage than do other individuals from Brazil we identified confidently as *O. macconnelli.* Crania in the Pará Sample are generally smaller and more gracile (figs. 89, 90), which is reflected in some cranial and dental measurements relative to those recorded for *O. macconnelli.* For example, compared with samples of *O. macconnelli,* the Pará series has, on average, a slightly shorter cranium; narrower interorbit, rostrum, and occiput; shorter diastema and bony palate; narrower incisive foramina; and shorter molar row (see appendix E). In dorsal view, the interorbit of *O. macconnelli* is noticeably wider relative to zygomatic breadth, and the rostrum is wider relative to its length in contrast to the Pará Sample (figs. 84, 89). Chromosomal differences also distinguish the few karyotyped samples of *O. macconnelli* and the Pará Sample (see below and table 13). Finally, we discovered that examples of *O. macconnelli* and specimens with the Pará morphology had been collected together at one site (locality 50 in gazetteer for *O. macconnelli*).

TABLE 41
Results of Discriminant Function Analysis of Population Samples of *Oryzomys macconnelli* (Samples 1–8), *Oryzomys nitidus* (Samples 9–17), and the *nitidus*-like Specimens (Sample 18) from Estado de Pará, Brazil
(Localities constituting each sample, and sample size, are listed in table 39, mean values for measurements in each sample are listed in appendix E, and specimens measured are identified in appendix F. See figs. 86 and 87.)

	Canonical variates		
Variable	First	Second	*F* (Sample)[a]
ONL	–0.00	0.12	40.0
ZB	–0.33	–0.27	70.5
IB	0.33	0.24	90.1
LR	0.05	–0.03	20.3
BR	0.22	0.07	20.9
LB	–0.07	0.31	50.8
HBC	–0.06	0.02	20.7
BZP	**–0.71**	0.18	260.0
LD	0.08	0.31	30.7
LBP	**0.77**	0.18	320.6
PPL	–0.22	–0.19	60.3
LIF	**–0.56**	0.27	140.3
BIF	**0.82**	–0.06	460.8
CLM1–3	**0.52**	–0.07	160.7
BM1	0.21	0.22	50.3
Canonical correlation	0.93	0.65	
Eigenvalue	6.72	0.71	
% Variance	69.2	7.3	

[a] All *F* values are significant at $P \leq 0.01$.

We reidentified the Pará Sample as *O. nitidus*. Chromosomal data strongly influenced this allocation. One example from sample 18 (MZUSP 27150) has $2n$ of 80 and FN of 86, which is like the karyotype of *O. nitidus* (also $2n = 80$ and FN = 86) but unlike karyotypes analyzed for *O. macconnelli* ($2n = 64$ or 76; FN = 64, 70, or 85; see fig. 109 and table 13).

However, neither does cranial morphology of the Pará series conform to that typical of *O. nitidus*. Their dissimilarities are reflected in the canonical variate and cluster analyses (figs. 86–88), as well as in comparisons of absolute mean values of variables and proportions between population samples of *O. nitidus* and the Pará series (fig. 84). Compared with the larger, more robust crania of *O. nitidus*, those of comparable age in the Pará Sample are smaller and more delicate (figs. 89, 90). The Pará series has, on average, a shorter cranium, narrower interorbit and occiput, narrower zygomatic plate, and shorter diastema and bony palate; the incisive foramina are also much shorter and slightly wider (appendix E). Proportional contrasts align specimens in the Pará Sample nearer to examples of *O. macconnelli* than to *O. nitidus* (fig. 84). Contrasted with *O. nitidus*, the Pará Sample has a narrower occiput (lambdoidal breadth) relative to zygomatic and interorbital breadths, a much narrower zygomatic plate relative to most other cranial measurements, a longer bony palate relative to occipitonasal length, and a relatively much shorter and wider incisive foramina. We were strongly influenced by these proportional contrasts between specimens of *O. nitidus* and those in the Pará Sample when initially identifying the Pará Sample as *O. macconnelli*, as well as the frequency of alisphenoid struts. Of 16 specimens from Pará surveyed, only one has slender alisphenoid struts, an infrequency similar to that observed in samples of *O. macconnelli* where struts are typically absent. By contrast, about half the specimens of *O. nitidus* surveyed have prominent and usually robust alisphenoid struts (table 38).

Results from analyses of sequence variation in base pairs of the mitochondrial cytochrome-b gene from samples of *O. macconnelli, O. nitidus, O. russatus*, and the Pará series (fig. 116) also corroborate the relationship among samples as revealed in the various morphometric analyses. Sequence results indicate that the Pará series does not affiliate with samples of *O. macconnelli*, but is nearer to specimens of *O. nitidus*; however, the percent sequence divergence of the Pará Sample from the latter species suggests separate species status (J. L. Patton, personal commun.; letter in AMNH Mammalogy Archives).

All evidence supports the hypothesis that the series from Pará represents a species different from either *O. macconnelli* or *O. nitidus*, but one likely more closely related to the latter. We name and describe it as a new species following the account of *O. macconnelli*.

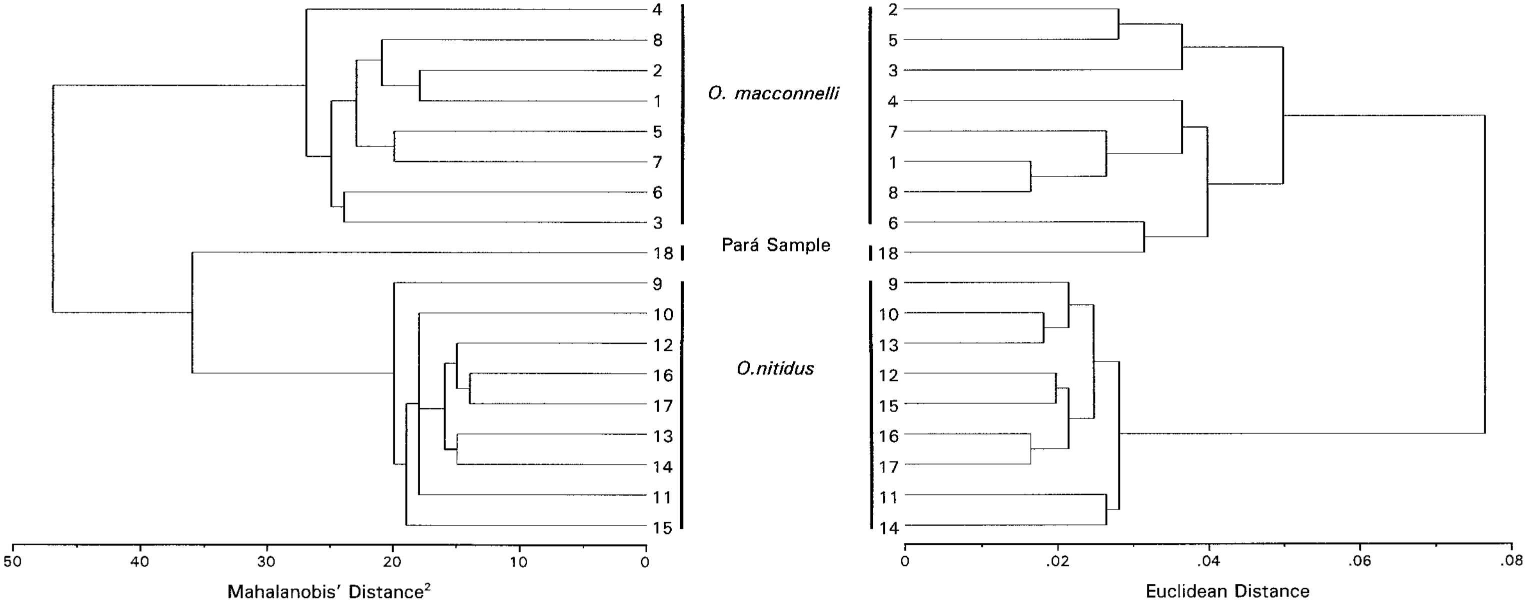

Fig. 88. UPGMA clustering of population samples of *Oryzomys macconnelli* (samples 1–8), *O. nitidus* (samples 9–17), and the series from Pará, Brazil (sample 18) generated from Mahalanobis' distances (D^2) among group centroids (see fig. 87) and Euclidean distances between samples based on log-transformed means of the 15 cranial and dental variables. Geographic origin and size of each sample are indicated in table 39, mean values for measurements of variables are listed in appendix E, and specimens measured are identified in appendix F.

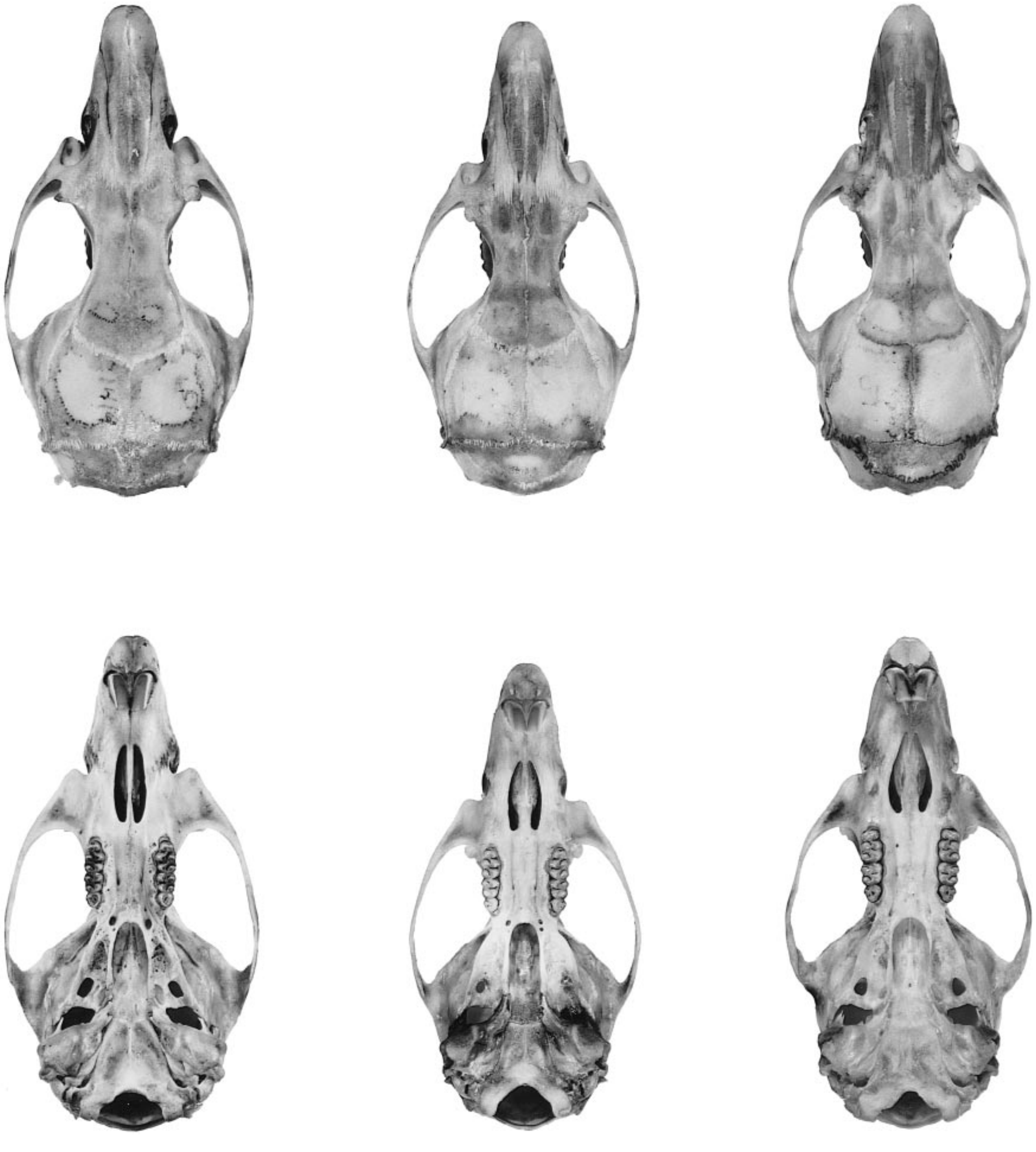

Fig. 89. Dorsal (**top**) and ventral (**bottom**) views of crania of species in the *Oryzomys nitidus* group. **Left,** *O. nitidus* (MNFS 1419, an adult male from Igarapé Porongaba, right bank Rio Juruá, Estado do Acre, Brazil); **middle,** an example from the Pará Sample (USNM 549552, an adult female from east bank of Rio Xingu, 52 km SSW Altamira, Estado de Pará, Brazil); **right,** *O. macconnelli* (USNM 448585, an adult male from San Ignacio de Yuruaní, Estado de Bolívar, Venezuela). ×2.

Oryzomys nitidus and *Oryzomys legatus*

In southern Bolivia, *Oryzomys nitidus* is replaced by populations currently recognized as *O. legatus* (Mares et al., 1981b; Musser and Carleton, 1993). Thomas (1925) named and described *O. legatus* and compared it to *O. intermedius* (the taxon for which we use the older name, *O. russatus*). We also regard the two forms to be closely related, and consider *legatus* as the Bolivian

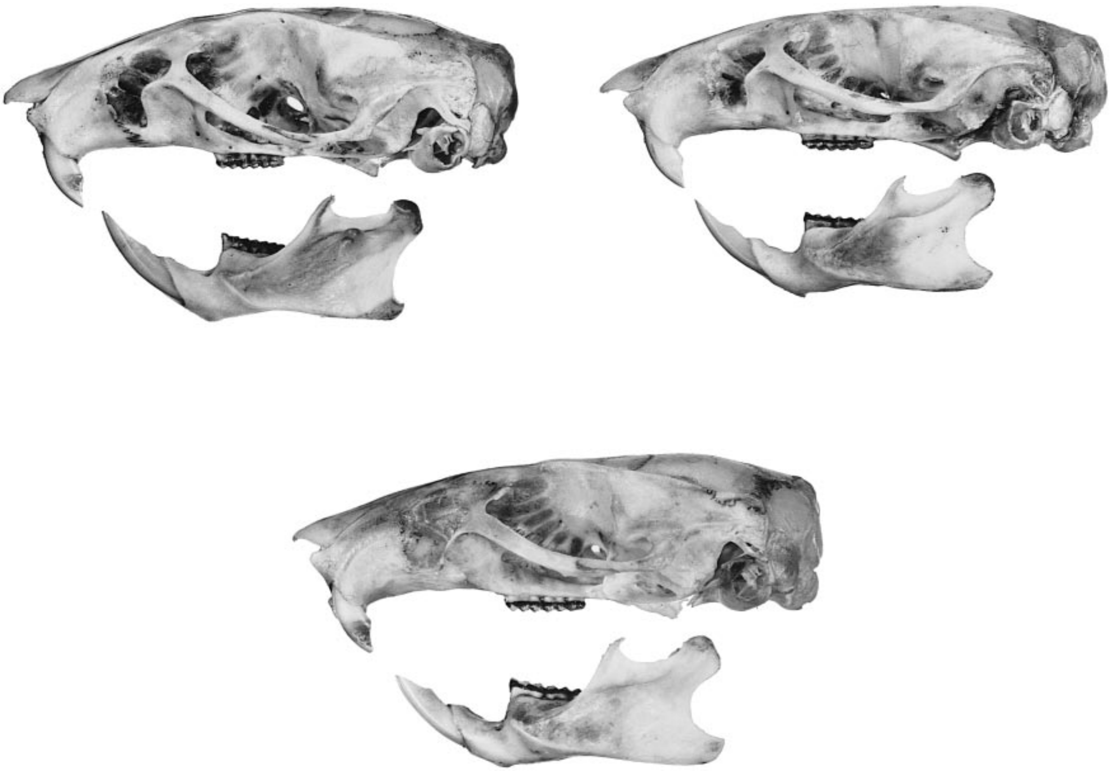

Fig. 90. Lateral views of crania and left dentaries of same specimens portrayed in figure 89 on opposite page. **Upper left,** *O. nitidus*; **upper right**, member of Pará Sample; **lower center**, *O. macconnelli*. ×2.

and Argentine component of *O. russatus*, an allocation we defend in our account of that species and *O. nitidus*. Here we focus only on the comparative distinctions between samples of *O. nitidus* and series from southern Bolivia and northern Argentina. We continue to identify these as *O. legatus* in the following discussion to emphasize our comparative concentration on the Bolivian and Argentine samples to the exclusion of the material representing *O. russatus* from eastern Brazil.

Our initial visual sorting of *O. nitidus*-like specimens uncovered several distinctive series from the departments of Chuquisaca and Tarija in southern Bolivia that are remarkable for their larger cranial and external size (see appendix E and table 37) and richer pelage having more intense ochraceous highlights. Subsequent principal components and discriminant function analyses confirmed that two species overlap in this geographic region–*O. nitidus* proper, as represented by specimens in sample 17, and another species currently listed as *O. legatus*, represented by samples 19 and 20 (table 39).

Principal components analyses of population samples 17, 19, and 20 (table 39) from southern Bolivia reveal two constellations of points, suggesting both the influence of age along the major axis of their regression lines and that of specific differences perpendicular to those axes (fig. 91). The large positive correlations of many variables on the first principal component—such as occipitonasal length, zygomatic breadth, length and breadth of rostrum, lambdoidal breadth, and breadth of zygomatic plate (fig. 91 inset, table 42)—affirm the overall larger size of the individuals from Chuquisaca and Tarija (see also fig. 92). In particular, those with moderate positive loadings on the first principal component, but large negative associations on the second component (interorbital

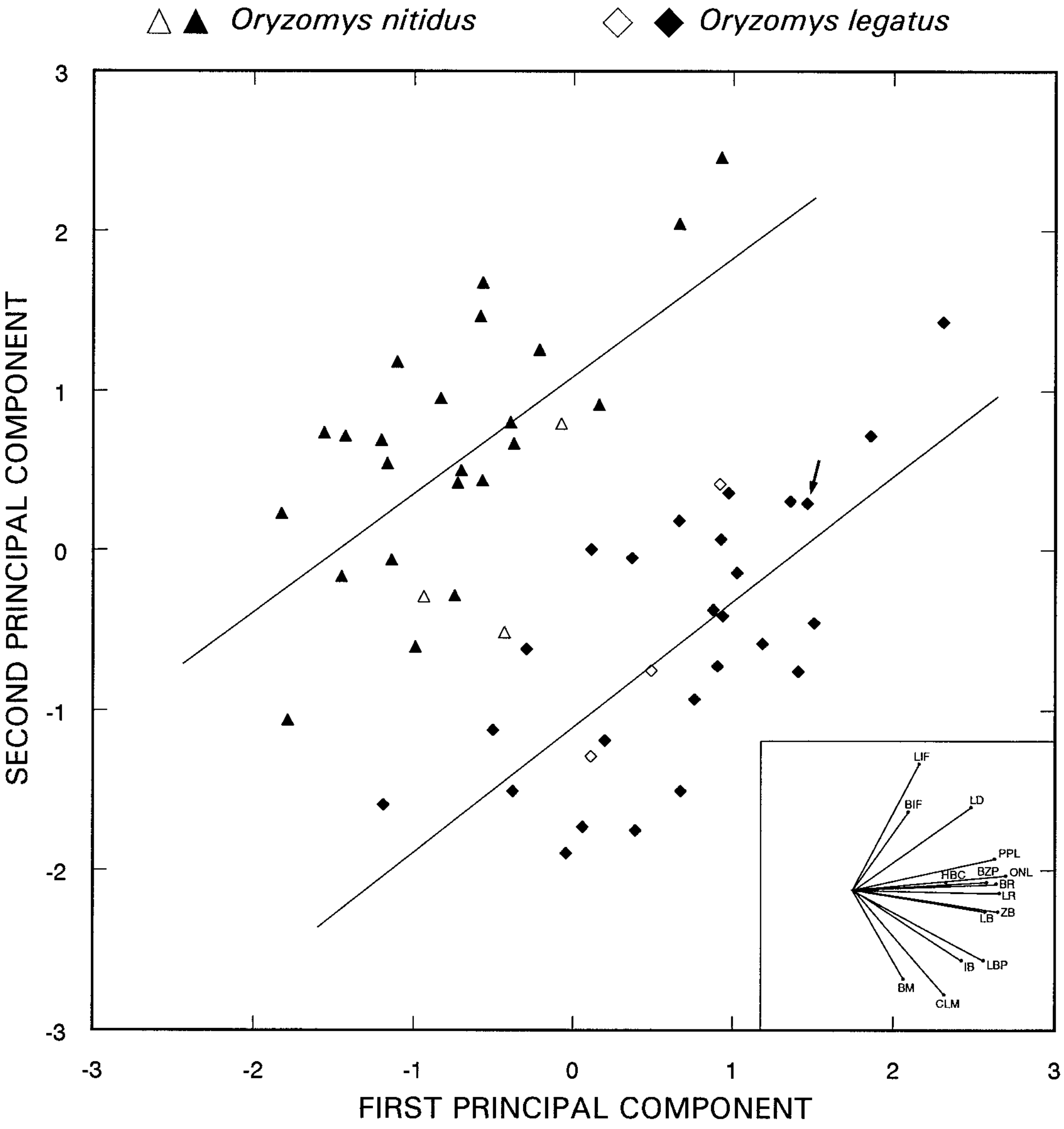

Fig. 91. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables and projected onto the first and second principal components, extracted from analysis of 52 adults from southern Bolivia, representing *Oryzomys nitidus* (sample 18) and samples currently recognized as *O. legatus* (samples 19 and 20). Open symbols identify specimens collected at 1 km NE Estancia Las Cuevas, Departamento de Santa Cruz (locality 140 and 151 in gazetteers for *O. nitidus* and *O. russatus*, respectively), a place where *O. nitidus* and *O. legatus* co-occur; arrow indicates holotype of *O. legatus*. Major axes of each constellation differ significantly in their Y-intercepts (1.17 versus -1.06, $P < 0.001$) but not in their slopes (0.78 versus 0.79, $P = 0.944$). **Inset:** Vectors of 15 cranial and dental variables corresponding to the magnitude and direction of their loadings (see table 42).

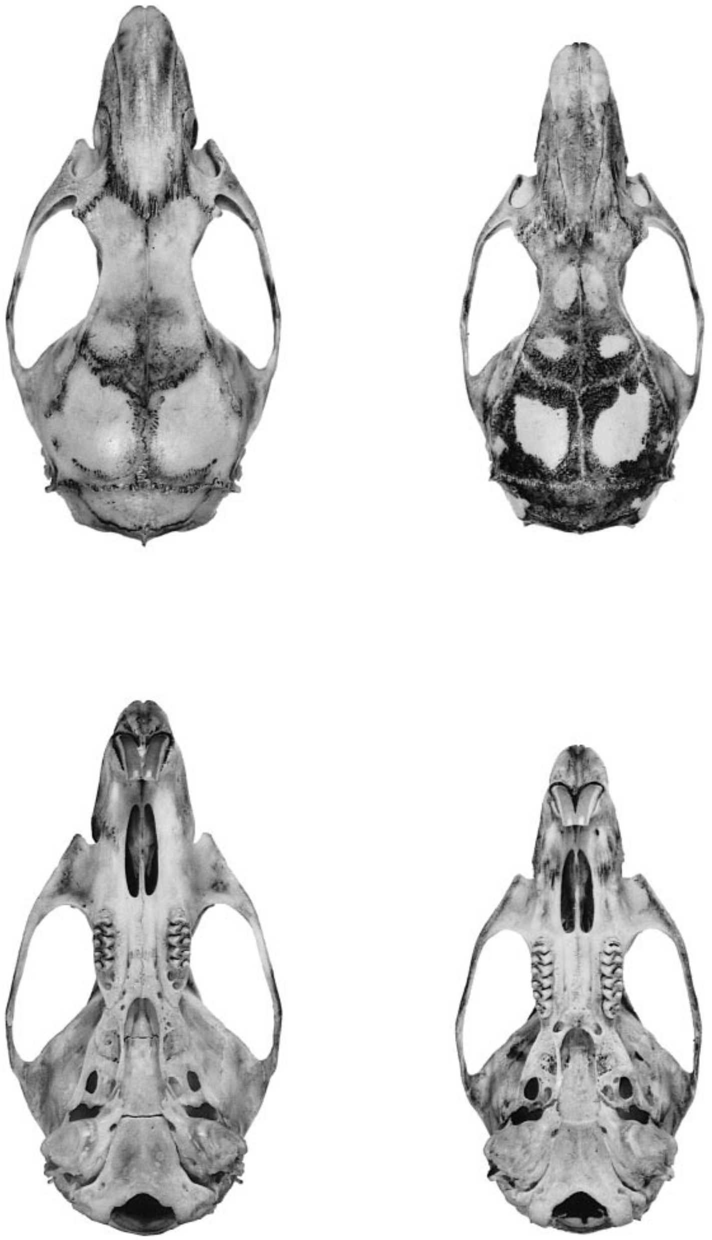

Fig. 92. Dorsal (**top**) and ventral (**bottom**) views of young adult crania from *Oryzomys legatus* (left pair, AMNH 264182) and *O. nitidus* (right pair, AMNH 264183) captured at 1 km NE Estancia Las Cuevas, Departamento de Santa Cruz, Bolivia (locality 140 and 151 in gazetteers for *O. nitidus* and *O. russatus*, respectively). ×2. See discussion in text.

breadth, length of bony palate, length of upper molar row, and breadth of first upper molar), emphasize the robustness of these dimensions in *legatus* (as compared to *O. nitidus*) and largely account for the oblique segregation of specimen scores in the scatterplot. In logical geometric correspondence to the longer bony palate, incisive foramina of *legatus* are shorter relative to those observed in samples of *O. nitidus* (this variable

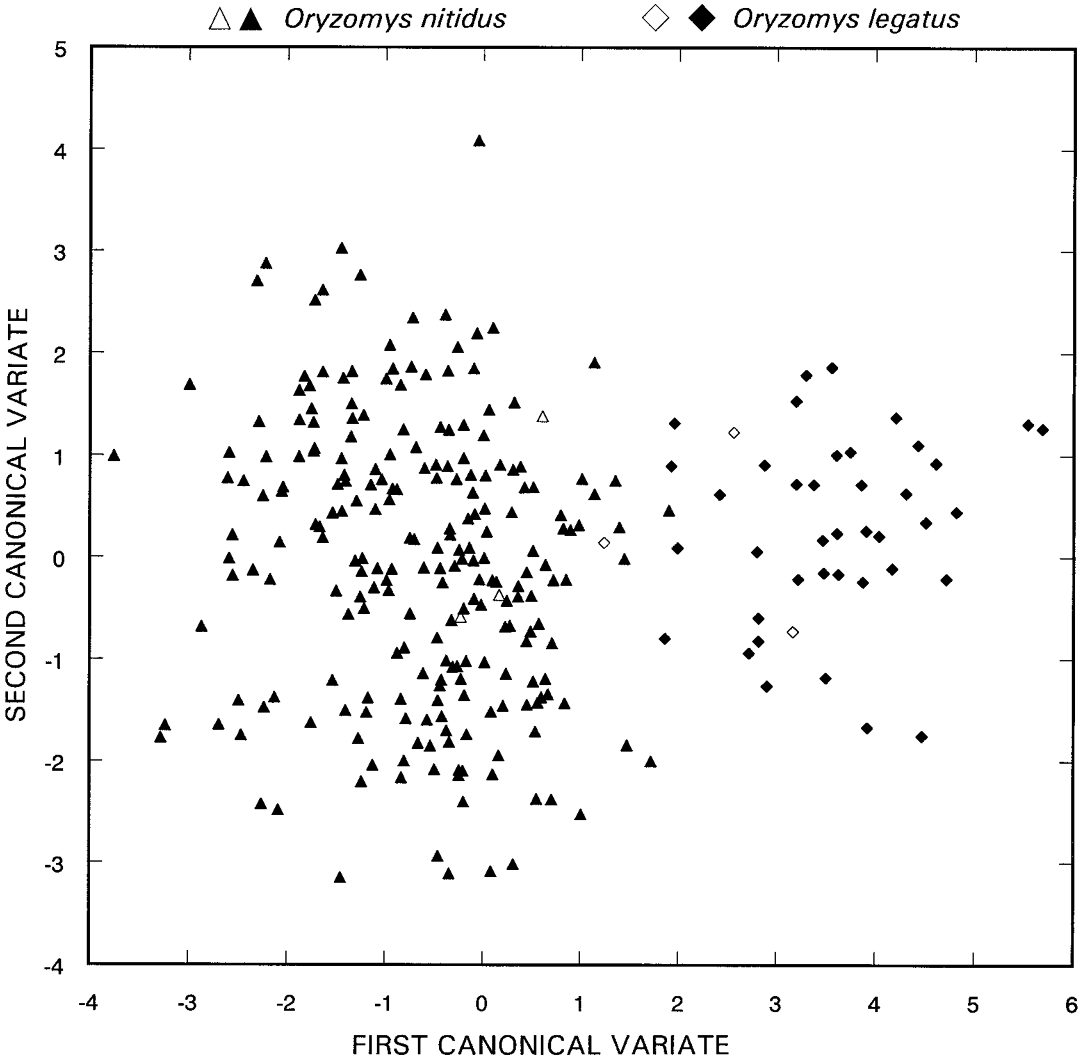

Fig. 93. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 43) and projected onto the first and second canonical variates derived from discriminant function analysis of 12 population samples representing *Oryzomys nitidus* (samples 9–17, *N* = 234) and *O. legatus* (samples 19–21, *N* = 40). See also figure 94 on opposite page. Open symbols represent specimens collected at 1 km NE Estancia Las Cuevas, Departamento de Santa Cruz, Bolivia (locality 140 and 151 in gazetteers for *O. nitidus* and *O. russatus,* respectively), where *O. nitidus* and *O. legatus* occur together.

is positive and somewhat large on the second principal component, also contributing to the obliquely drawn line of separation).

Note the placement of seven specimens in the principal components scatterplot. One represents the holotype of *legatus* (indicated by an arrow in fig. 91) and clearly falls within the cloud of scores derived from the Chuquisaca and Tarija samples. Three other data points represent individuals from 1 km NE of Estancia Las Cuevas (locality 140 in gazetteer for *O. nitidus*) that are examples of *legatus* (AMNH 264182, 264184; MSB 67321), and these points also mingle within

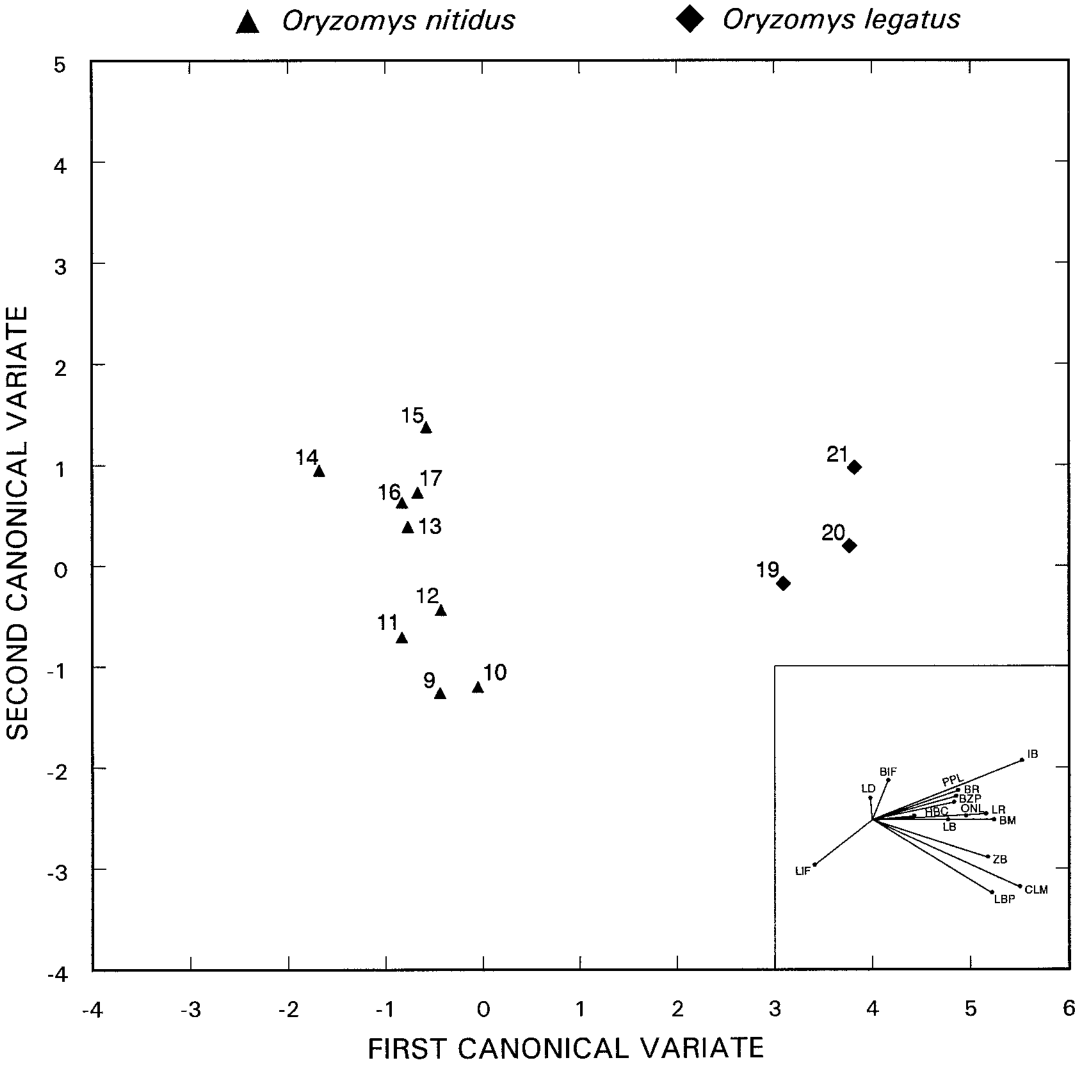

Fig. 94. Plot of group centroids on first two canonical variates derived from discriminant function analysis of 12 samples representing *Oryzomys nitidus* (samples 9–17) and *O. legatus* (samples 19–21). See also figure 93 on opposite page. **Inset:** Vectors of 15 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (see table 43). Size of samples and localities that constitute each sample are listed in table 39.

the cluster of scores representing *legatus*. The last three of the seven scores identify specimens from that same locality (AMNH 264183, MSB 67322 and 67323), but their points intermingle with those derived for the remainder of specimens in sample 17, all of which represent individuals with smaller, less robust crania that we identify as *O. nitidus*. We interpret these morphologies and the corresponding distribution of scores from near Estancia Las Cuevas to represent sympatry between two species.

A discriminant function analysis of our nine population samples of *O. nitidus* from Perú and Bolivia (samples 9–17; table 39), combined with the three samples of *legatus* from southern Bolivia and northern Argentina (19–21), broadens our comparative geographic scope along the eastern Andean foothills. Two discrete clusters are apparent, ei-

TABLE 42

Results of Principal Components Analysis Performed on 55 Specimens from Southern Bolivia, Representing *Oryzomys nitidus* (Sample 17) and Samples Currently Recognized as *Oryzomys legatus* (Samples 19 and 20)

(Localities constituting population samples 17, 19, and 20 are listed in table 39, mean values for measurements in each sample are listed in appendix E, and specimens measured are identified in appendix F. See fig. 91.)

	Principal components	
Variable	First	Second
ONL	**0.97**	0.09
ZB	**0.92**	–0.14
IB	0.68	**–0.45**
LR	**0.93**	–0.03
BR	**0.91**	0.04
LB	**0.84**	–0.13
HBC	0.59	0.05
BZP	**0.85**	0.04
LD	0.73	0.53
LBP	0.79	**–0.49**
PPL	**0.90**	0.21
LIF	0.42	**0.81**
BIF	0.35	0.46
CLM1–3	0.58	**–0.67**
BM1	0.32	**–0.57**
Eigenvalue	0.028	0.008
% Variance	570.8	160.5

TABLE 43

Results of Discriminant Function Analysis of Population Samples of *Oryzomys nitidus* (Samples 9–17) and Samples Currently Recognized as *Oryzomys legatus* (Samples 19–21)

(Localities constituting each sample, and sample size, are listed in table 39, mean values for measurements in each sample are listed in appendix E, and specimens measured are identified in appendix F. See figs. 93 and 94.)

	Canonical variates		
Variable	First	Second	*F* (Sample)[a]
ONL	0.47	0.04	6.4
ZB	0.58	–0.16	9.5
IB	**0.74**	0.32	19.8
LR	0.57	0.05	9.9
BR	0.42	0.14	5.4
LB	0.38	0.01	4.8
HBC	0.21	0.03	2.6
BZP	0.40	0.11	5.0
LD	–0.01	0.13	2.7
LBP	**0.60**	–0.37	13.3
PPL	0.43	0.17	5.2
LIF	–0.29	–0.20	5.8
BIF	0.08	0.20	5.0
CLM1–3	**0.74**	–0.33	21.0
BM1	**0.61**	0.00	11.7
Canonical correlation	0.84	0.67	
Eigenvalue	2.38	0.81	
% Variance	55.4	18.9	

[a] All *F* values are significant at $P \leq 0.01$.

ther in the scatter of individual specimen scores (fig. 93) or of group centroids (fig. 94), on the first two canonical variates extracted from the discriminant function. Again, the larger size of individuals identified as *legatus* and the correspondingly smaller individuals of *O. nitidus* are reflected in the nearly uniform positive loadings of cranial and dental variables on the first canonical variate (fig. 94 inset, table 43); variation in interorbital breadth, length of bony palate, length of upper molar row, and breadth of first upper molar are most influential (the vectors longest) in the spread of specimen scores along the first axis. Loading for length of incisive foramina is negative (although modest in magnitude) on the first canonical variate, suggesting the relatively longer incisive foramina characteristic of *O. nitidus* (absolute mean values for length of incisive foramina are similar or slightly smaller in samples of *legatus* compared with those of *O. nitidus*; appendix E). Variation in two other variables from the same cranial region—length of diastema and breadth of incisive foramina—negligibly affect separation of *O. nitidus* and *legatus* (both are small and their loading vectors are oriented perpendicular to the greatest hiatus between the species centroids; fig. 94 inset, table 43).

The abrupt shift in overall cranial size in southern Bolivia can also be appreciated in a diagram of first canonical variate parameters arranged north to south from central Perú to northern Argentina (fig. 95). This pattern, along with separation among individual specimen scores in the principal components analysis (fig. 93) and qualitative sorting of crania (fig. 92) and skins (table 44), supports the occurrence of sympatry of *legatus* with *O. nitidus* and validates the status of these

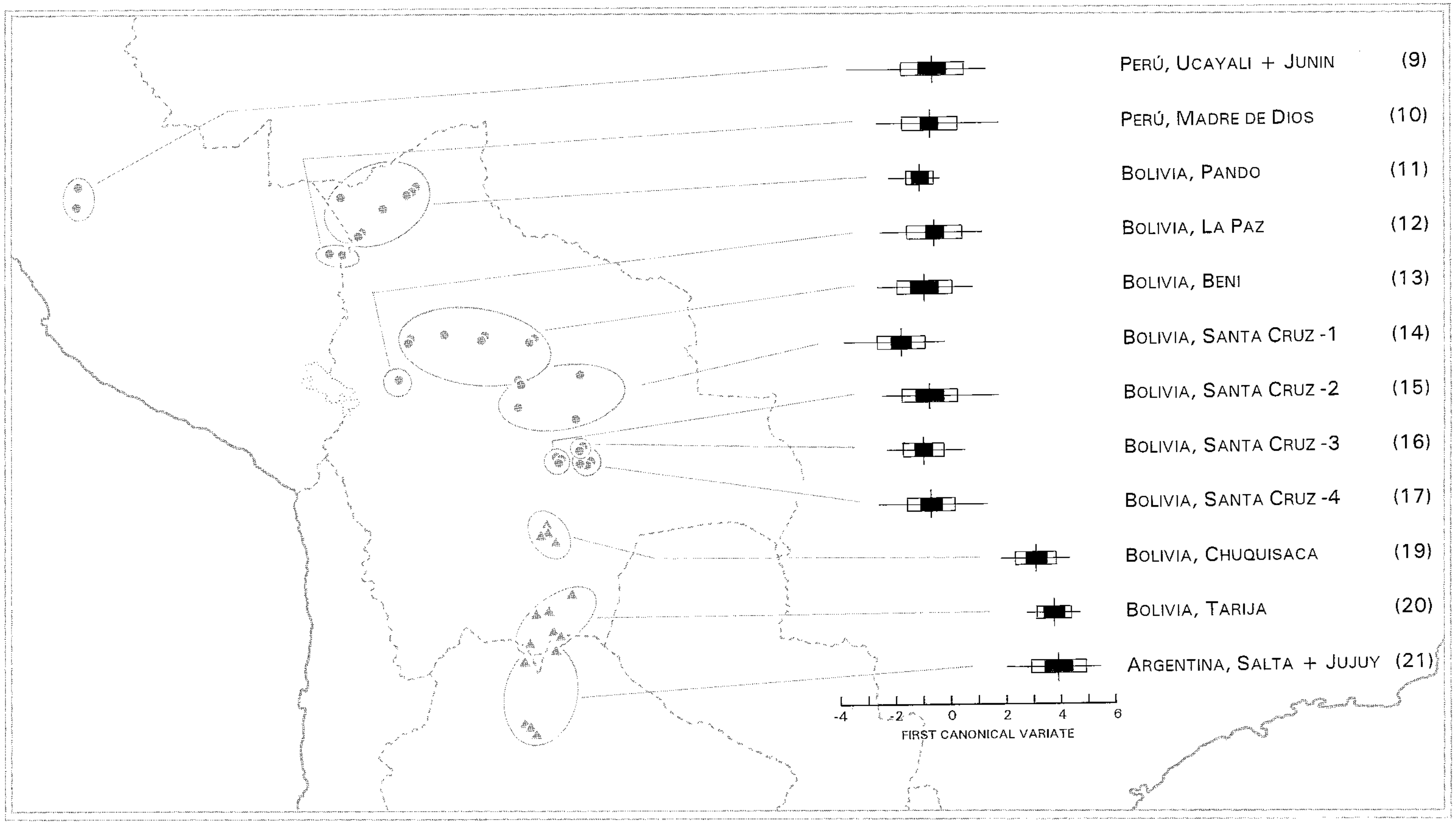

Fig. 95. Dice-Leraas diagrams of first canonical variate parameters (see figs. 93 and 94) for population samples of the *Oryzomys nitidus* group (samples 9–17, 19–21; table 39) arranged on a southward transect from central Perú to northern Argentina. Vertical line corresponds to the sample mean, the horizontal line the sample range, the open rectangle ± one standard deviation, and the closed rectangle ± two standard errors of the mean. Sample sizes and localities constituting each population sample are identified in table 39, descriptive statistics for each sample are listed in appendix E, and specimens measured are identified in appendix F.

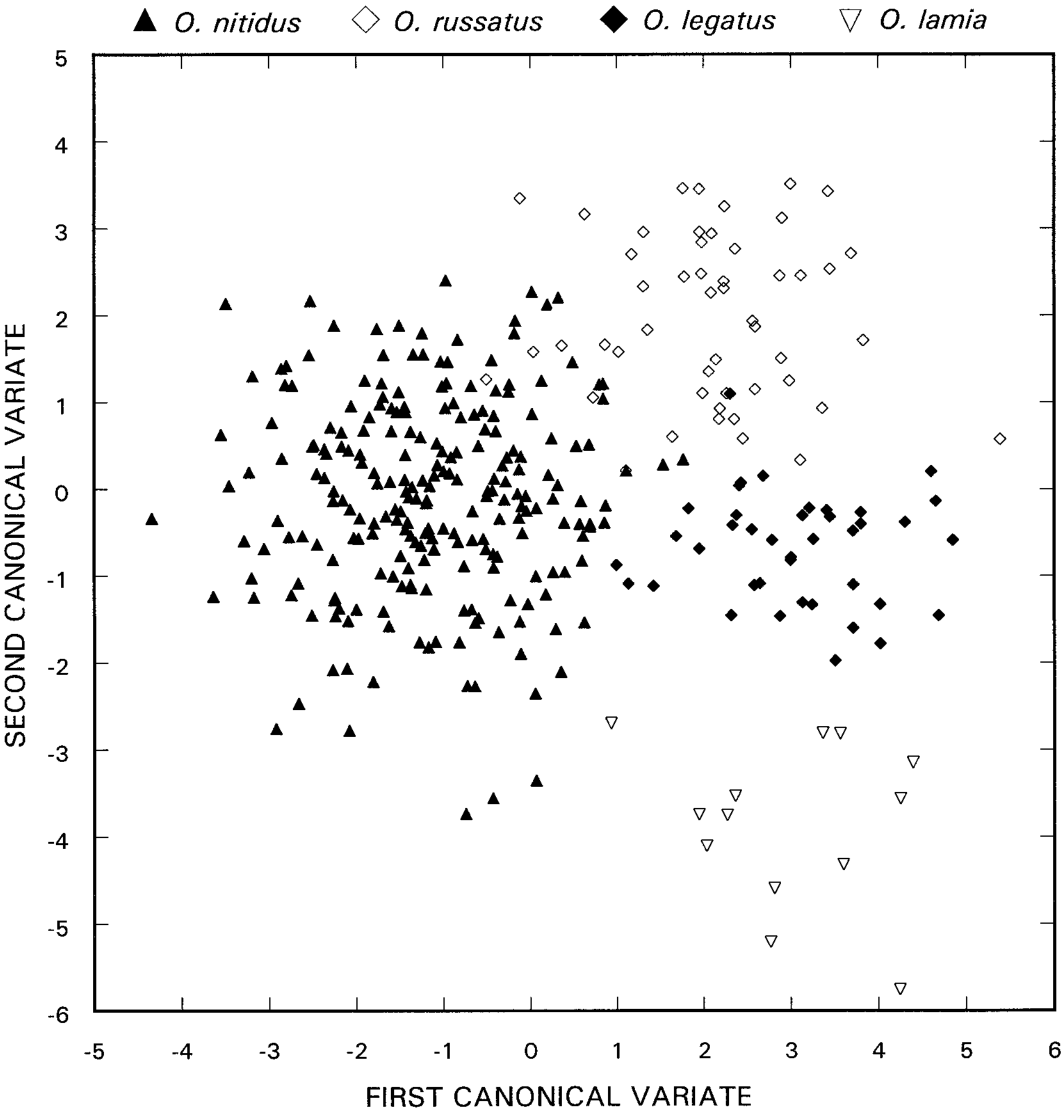

Fig. 96. Individual specimen scores based on log-transformed values of 13 cranial and 2 dental variables (see table 45) and projected onto the first and second canonical variates derived from discriminant function analysis of 15 population samples (table 39) representing *Oryzomys nitidus* (samples 9–17, *N* = 234), *O. russatus* (samples 22 and 23, *N* = 50), and the taxa recognized as *O. legatus* (samples 19–21, *N* = 40) and *O. lamia* (sample 24, *N* = 24). Also see figure 97 on opposite page.

populations as a species separate from *O. nitidus*.

At the place where the two kinds co-occur, the examples of *legatus* contrast with those of *O. nitidus* in their generally larger size (especially length of hind foot) and greater body weight (table 44), as well as in most cranial dimensions, as indicated above by the multivariate analyses, and by their relatively shorter incisive foramina; to our eyes, the crania of *legatus* appear larger and more robust (fig. 92).

Pelage coloration is basically similar in the two sets of specimens from southern Bolivia, but those identified as *legatus* have much brighter hues to the dorsal coat, where the

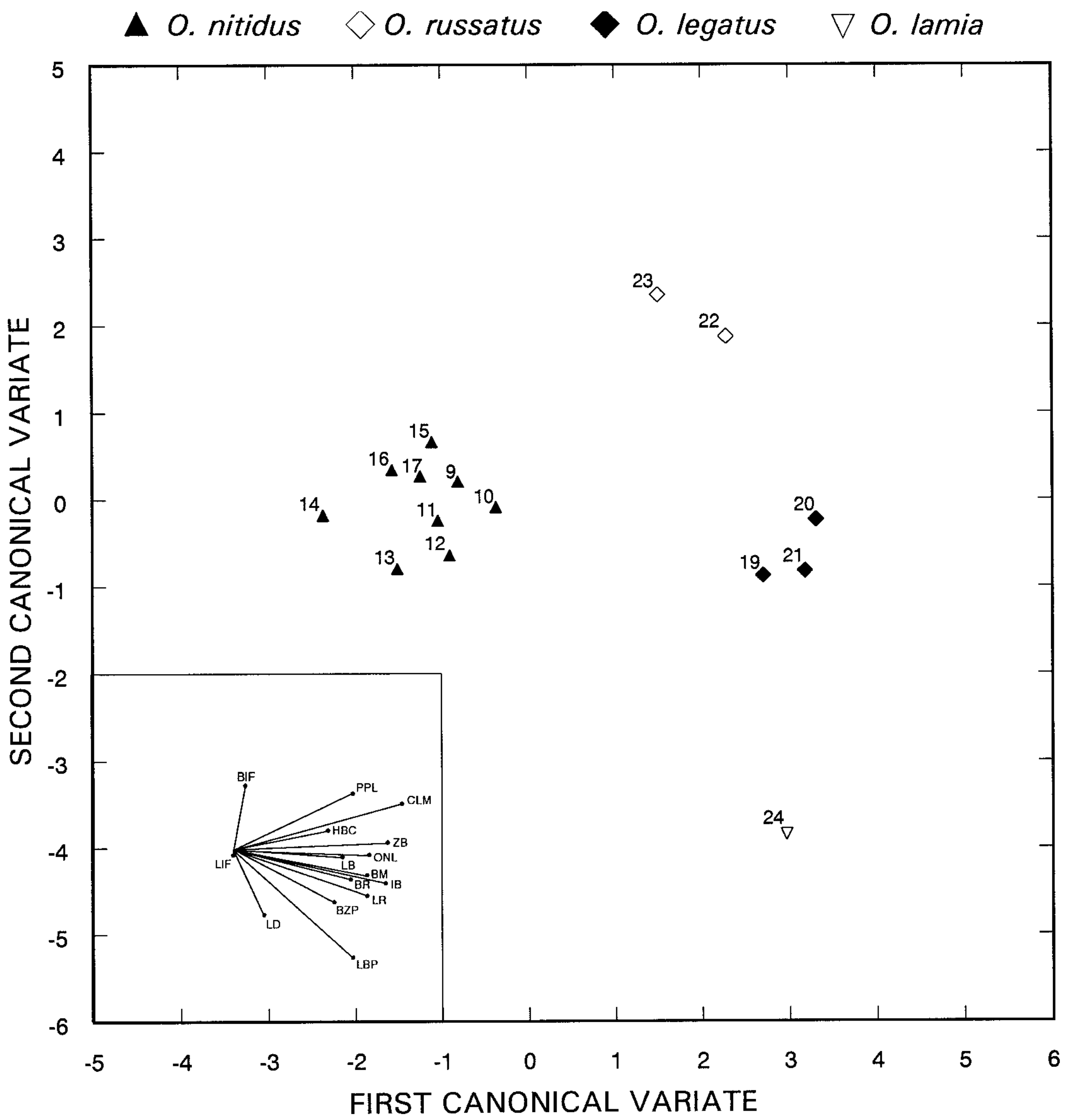

Fig. 97. Plot of group centroids on first two canonical variates derived from discriminant function analysis of 15 samples (table 39) representing *Oryzomys nitidus* (samples 9–17), *O. russatus* (samples 22 and 23), *O. legatus* (samples 19–21), and *O. lamia* (sample 24). **Inset:** Vectors of 15 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (also see table 45).

rich ochraceous tawny tones along sides of the head and body extend up over the back and rump on which they are slightly darkened by the pattern of fine spotting from black-tipped guard hairs. In the examples of *O. nitidus,* by contrast, the back and rump are darker, exhibit more subdued tones, and the brighter ochraceous tawny hues are restricted to sides of the body just above the demarcation between upperparts and underparts. These dimensional and chromatic contrasts also distinguish specimens of *legatus* from those of *O. nitidus* in the geographic areas where we have no records of sympatry.

The meager information about habitat near Estancia Las Cuevas where the specimens of

TABLE 44

External Measurements and Weight from Specimens of *Oryzomys nitidus* and *Oryzomys legatus* Captured at the Same Locality in Southern Bolivia (1 km NE Estancia Las Cuevas, Departamento de Santa Cruz; locality 140 in gazetteer for *O. nitidus*)

		Measurement (mm) and weight (g)[a]				
Species and specimens	Age	LHB	LT	LHF[a]	LE	W
O. nitidus						
MSB 67323-F	Adult	141	143	32	22	68
MSB 67322-F	Adult	146	—	32	22	71
AMNH 264183-F	Young adult[b]	130	147	31	20	67
O. legatus						
AMNH 264185-M	Adult	153	155	34	23	91
AMNH 264182-M	Young adult[b]	129	135	34	21	85
AMNH 264184-M	Very young adult[b]	132	132	32	23	62
MSB 67321-M	Very young adult[b]	148	155	35	21	66

[a] Taken from labels attached to skins; measurements of hind feet were checked by G. G. Musser.

[b] The three specimens of *O. legatus* are in adult pelage, but exhibit patches throughout the dorsal coat where adult hairs had not proliferated to their full length. The young adult example of *O. nitidus* is fully covered by an adult coat.

O. nitidus and *legatus* were captured (a specimen of each was taken in the same line of traps) was presented above under the subsection dealing with documented sympatry between *O. nitidus* and other species. Additional field surveys in that region should be undertaken to investigate the ecological preferences of the two species.

As Thomas (1925) indicated, the morphological affinities of samples from southern Bolivia and northern Argentina we identify as *legatus* are with populations in eastern Brazil that he knew as *O. intermedius*, and for which we use the name *O. russatus*. In the following section, we develop the hypothesis that *legatus* is a geographic representative of *O. russatus*, which we compare to *O. nitidus*.

Oryzomys nitidus and *Oryzomys russatus*

When specimens of the Pará Sample and of *O. macconnelli* are omitted from consideration of the *O. nitidus* group, there remain two clusters of specimens, distinguished largely by differences in size of external and cranial dimensions. We identify the smaller bodied rat as *O. nitidus*, which we have already defined relative to samples of *O. macconnelli*, the Pará Sample, and those currently known as *O. legatus*. The definition of *O. nitidus* is incomplete, however, without contrasting it with the group of larger bodied rats, samples of which have been referred to in the literature as *O. intermedius* (= *russatus*), *O. lamia*, and *O. legatus*. All of these taxa represent populations characterized by moderately large body size and brightly colored pelage. The greater body size generally mirrors that observed between *O. nitidus* and *O. legatus*, with *O. lamia* being perhaps another step larger. Whereas the contrast in size between *O. nitidus* and *O. legatus* in southern Bolivia and the taxonomic significance of *O. nitidus* are reinforced by the criterion of sympatry, we lack such evidence for the widely scattered series available for *O. lamia* (riverine forests in the Cerrado of south-central Brazil), *O. russatus* (tropical and subtropical rain forests of southeastern Brazil), and *O. legatus* from other parts of its range in the Andean forests of extreme southern Bolivia and northern Argentina.

In the absence of documented sympatry between *O. nitidus* and members of the group containing larger-bodied animals, we turned to discriminant function analysis to test our perception (derived from sorting specimens) that two groups actually exist. Two primary clusters (15 groups defined a priori; table 39) are apparent in the scatter of individual scores and group centroids projected upon the first and second canonical variates extracted (figs. 96, 97). Here, the *legatus* series from southern Bolivia and northern Argentina are shown to be morphologi-

TABLE 45

Results of Discriminant Function Analysis of 15 Population Samples Representing *Oryzomys nitidus* (Samples 9–17), *Oryzomys russatus* (Samples 22 and 23), and Series Currently Identified as *O. legatus* (Samples 19–21) and *O. lamia* (Sample 24)

(Localities constituting each sample and size of sample are listed in table 39, mean values for measurements in each sample are presented in appendix E, and specimens measured are identified in appendix F. See figs. 96 and 97.)

	Canonical variates		
Variable	First	Second	*F* (Sample)[a]
ONL	0.67	−0.04	18.0
ZB	0.75	−0.03	24.1
IB	0.74	−0.17	24.4
LR	0.65	−0.23	16.9
BR	0.57	−0.14	13.1
LB	0.53	−0.04	9.4
HBC	0.46	−0.09	9.6
BZP	0.49	−0.26	9.9
LD	0.15	−0.32	6.9
LBP	0.58	−0.53	20.5
PPL	0.58	0.27	14.0
LIF	0.00	−0.03	8.3
BIF	0.06	0.31	8.1
CLM1–3	0.82	0.22	32.7
BM1	0.65	−0.14	14.5
Canonical correlation	0.88	0.77	
Eigenvalue	3.37	1.43	
% Variance	49.2	20.8	

[a] All *F* values are significant at $P \leq 0.001$.

cally closer to *lamia* and *russatus* from geographic regions to the east than they are to samples of *O. nitidus*. All three *russatus*-sized forms are distinguishable from those samples representing *O. nitidus* by their more robust crania and longer molar rows; 12 of the cranial and dental variables (excluding only length of diastema and length and breadth of incisive foramina) load moderately strongly and positively on the first canonical variate (fig. 97 inset, table 45). This fundamental resemblance in size among samples of *legatus*, *lamia*, and *russatus* and their clear contrast to the smaller *O. nitidus* can also be seen in the illustrations of crania in figures 98 and 99. Cluster diagrams derived from Mahalanobis' and Euclidean distances confirm the distinctiveness of *O. nitidus* relative to samples of *russatus*, *legatus*, and *lamia* (fig. 100).

The scores of various holotypes and paratypes derived from posterior probabilities of group membership are shown in the plot of group centroids for all samples of the *O. nitidus* group (fig. 114). The classification of types is consistent with our interpretation of species limits and their probable synonymies (see Taxonomic Summary). The score for the holotype of *boliviae* nestles within the group centroids for samples of *O. nitidus*; scores for holotypes of *lamia*, *intermedia*, *legatus*, and *russatus* fall within the cluster of centroids of the larger bodied animals we identify as *O. russatus*, as do paratypes of *kelloggi* (described as a distinct species by Ávila-Pires, 1959a) and *moojeni* (described as a subspecies of *O. ratticeps* by Ávila-Pires, 1959b).

Among the series of larger bodied animals, the sample of *lamia* is isolated along the second canonical variate in figures 96 and 97; most of the same 12 cranial and dental variables are small but consistently negative on this axis (table 45), reflecting the larger crania of *lamia* compared with those of *legatus* and *russatus*. Breadth of incisive foramina and length of diastema load heavily on the second canonical variate, revealing that the sample of *lamia* has long but particularly narrow incisive foramina and a long diastema. Also, the diagonal direction of many loading vectors (large size expressed as positive on the first canonical variate, small to moderate indicated as negative on the second canonical variate) toward *lamia* also points to its larger cranial size compared to the samples of *legatus* and *russatus*, and especially to samples of *O. nitidus* (fig. 97 inset, table 45). The separation of *lamia* is also emphasized by the cluster diagrams derived from Mahalanobis' and Euclidean distances (fig. 100). Also, the relationships shown there based on Mahalanobis' distances among the group centroids (see also fig. 97) preserve the integrity of *legatus* and *russatus*, whereas phenetic resemblance based on mean cranial size (Euclidean distance) questions their segregation as separate entities. Neither coefficient of similarity weakens the homogeneity among samples we recognize as *O. nitidus* or

Fig. 98. Dorsal views of adult crania contrasting examples from the *Oryzomys nitidus* group. From left to right, *O. nitidus* (KU 144471, Reserva Cuzco Amazónica, Departamento de Madre de Dios, Perú), *O. russatus* (AMNH 203073, Além Paraíba, Estado de Minas Gerais, Brazil), *O. lamia* (AMNH 134763, Anápolis, Estado de Goiás, Brazil), and *O. legatus* (AMNH 263885, Río Limon, Departamento de Chuquisaca, Bolivia). ×2. We regard the examples currently referred to as *lamia* and *legatus* to represent geographic segments of *O. russatus*. See discussion in text.

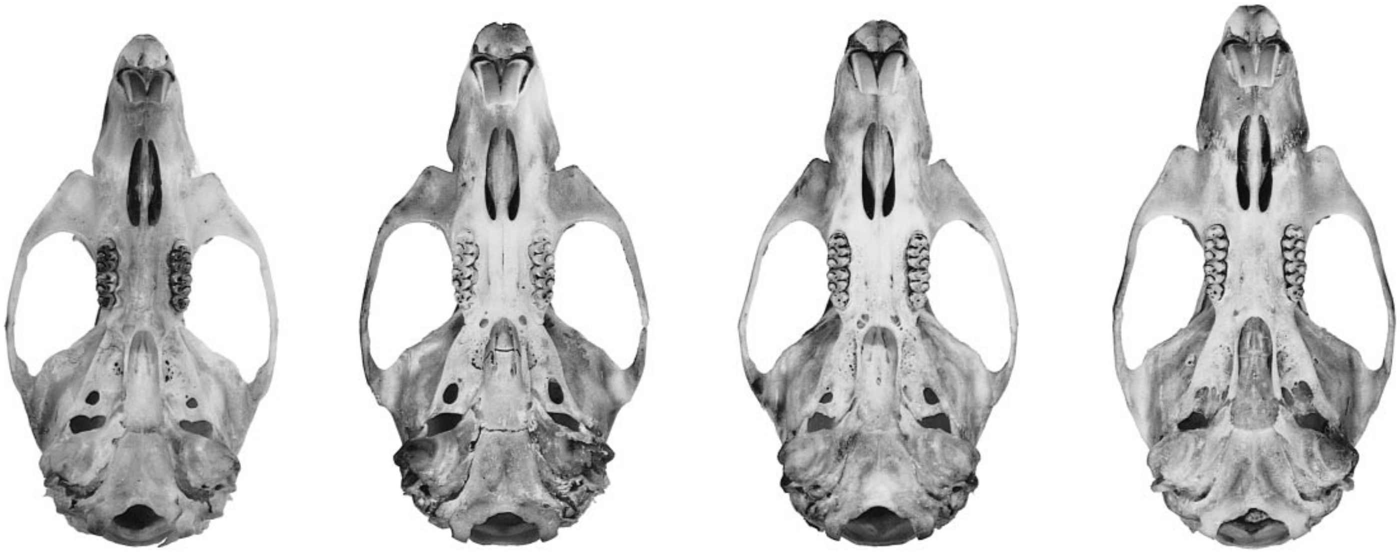

Fig. 99. Ventral view of same crania shown in figure 98 on opposite page. From left to right, *O. nitidus*, *O. russatus*, *O*, *lamia*, and *O. legatus*. ×2.

their collective isolation from *russatus*, *legatus*, and *lamia*.

In relation to samples of *O. nitidus*, large body size unites samples of *legatus*, *lamia*, and *russatus*. However, appreciable range in body size (as estimated by cranial dimensions), which we interpret as geographic variation, exists between population samples of those three taxa. Examples of *lamia* are larger than those of *russatus*, whereas specimens of *legatus* are intermediate in size. Recognizing each of these forms as a distinct species would be a reasonable interpretation of the ordination and clustering results discussed above. However, we advance the hypothesis that samples of these three large-bodied taxa represent a single species for several reasons. First, our sample sizes of *russatus*, *legatus*, and *lamia* are generally small and restricted in geographic scope, and not at all comparable to the large series and extensive geographic coverage available for *O. nitidus*. We measured most specimens of *legatus* and *lamia* that are preserved in collections of museums, but more specimens of *russatus* are available in Brazilian museums that we did not utilize. Second, available samples of *legatus* and *lamia* are biased in age categories. Most examples of *legatus* are young or very young adults. The greater average overall cranial size indicated for the series of *lamia* is influenced by about half the series from Anápolis that consists of large old adults. Third, documented geographic distributions of *russatus*, *legatus*, and *lamia* are complementary, not overlapping. Finally, in discriminant function analysis of all 24 population samples, the pattern of intersample variation among *russatus*, *legatus*, and *lamia*, relative to clusters representing the other three species (*O. nitidus*, *O. macconnelli*, and the Pará Sample), suggests that their constellation also represents a single species (figs. 113, 114). This conclusion admittedly is not evident when samples of only those three large-bodied taxa and *O. nitidus* are compared (figs. 96, 97).

Our hypothesis can be tested by field surveys designed to obtain larger samples equivalent in age composition from the known geographic ranges of *russatus*, *legatus*, and *lamia*, as well as from unsampled regions of suitable, but currently unsampled, habitat between those distributions. Our samples of *legatus* and *lamia* seem more similar in morphology to one another than to available series of *russatus*. Both *legatus* and *lamia* have slightly larger and more robust crania compared with those of *russatus* (figs. 98, 99), and they exhibit a brighter dorsal coat due mostly to the pronounced ochraceous tones along the sides of head and body. Acquisition of larger samples from a more extensive region would be critical in determining relationships among populations from southern Bolivia, south-central Brazil, and eastern Brazil that for now we embrace as a single species.

This species, for which the oldest available scientific name is *O. russatus*, is distinguished from samples of *O. nitidus* by larger average size in most mensural variables (see table 37 and appendix E) and, on average, by a brighter dorsal pelage, especially along sides of head and body. The few chromosomal samples derived from each species are indistinguishable in karyotype composition at the gross level of preparation ($2n = 80$ and FN = 86, table 13).

Analysis of sequence variation in base pairs of the cytochrome-b gene from samples of the *O. nitidus* group reinforces the morphological distinctions observed between *O. nitidus* and *O. russatus*, chromosomal similarity aside (fig. 116). In the maximum parsimony tree, samples of *O. russatus* actually associate more closely with those of *O. macconnelli* than with specimens of *O. nitidus*.

GEOGRAPHIC VARIATION

In the early phase of our study, while sorting and measuring specimens of *O. nitidus*, we were impressed by the low variation that seemed to exist within and among population samples, except for the series from Pará. This impression is similarly conveyed by the multivariate analyses. Results of cluster analysis with Mahalanobis' distance as a measure of resemblance underscore the physical dissimilarity of the sample from Pará, which at one time we had identified as *O. nitidus*, as compared with population samples of *O. nitidus* from Perú and Bolivia (fig. 101). By contrast, the discrimination among samples of true *O. nitidus* is not appreciable in multivariate

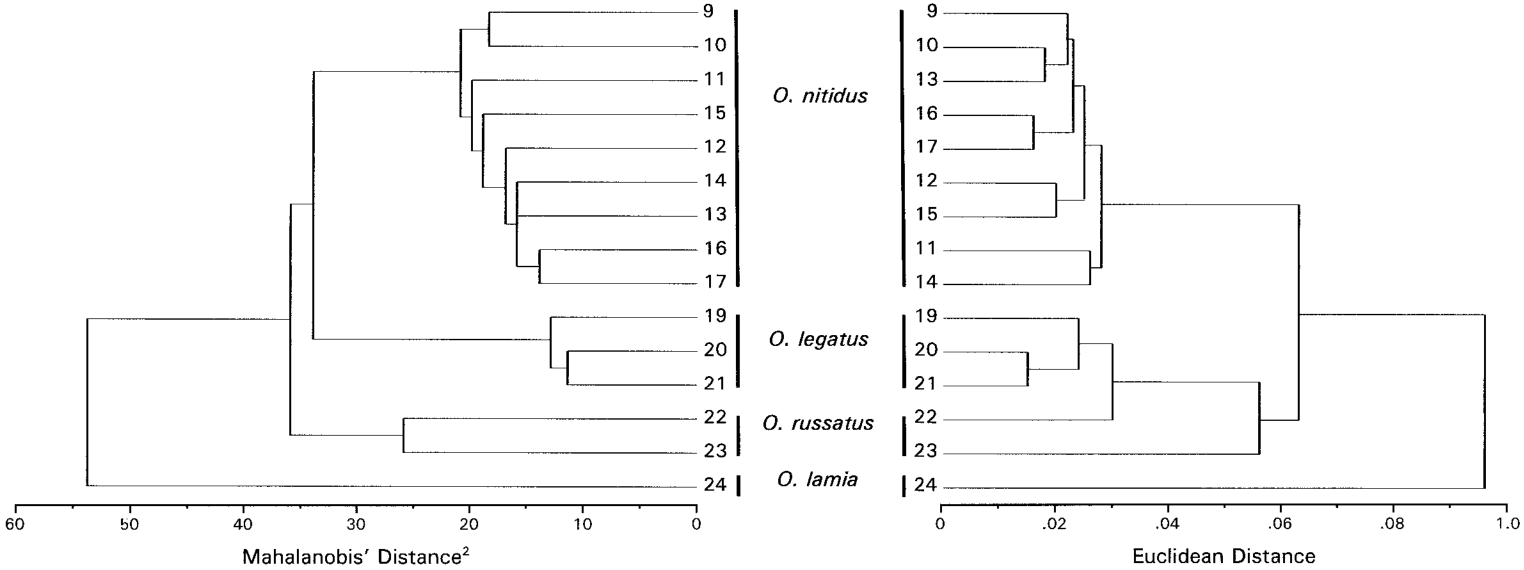

Fig. 100. UPGMA clustering of 15 population samples of *Oryzomys nitidus* (samples 9–17) and *O. russatus* (samples 19–24) generated from Mahalanobis' distances (D^2) among group centroids (see fig. 89) and Euclidean distances between samples based on log-transformed means of 15 cranial and dental variables. Geographic origins and sizes of samples are indicated in table 39, mean values for measurements of variables are listed in appendix E, and specimens measured are identified in appendix F.

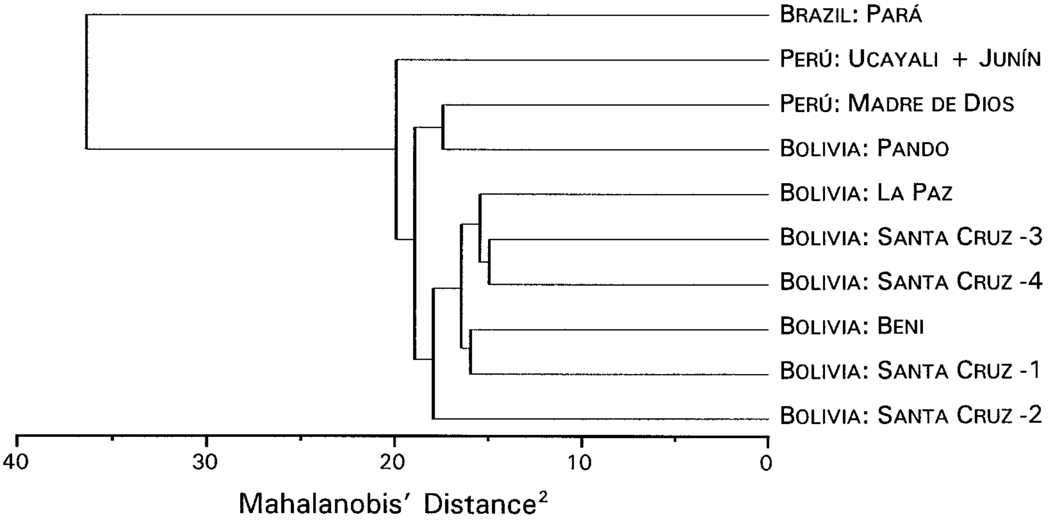

Fig. 101. UPGMA clustering of nine population samples of *Oryzomys nitidus* and sample 18 from central Pará, Brazil, generated from Mahalanobis' distances (D^2) among group centroids. Geographic origins and sizes of samples are indicated in table 39, mean values for measurements of variables are listed in appendix E, and specimens measured are identified in appendix F. See discussion in text.

space. Still, there is a suggestion of geographic pattern: the population samples from Perú (population samples 9 and 10; table 39) and northern Bolivia (sample 11) are more closely associated among themselves than to samples from farther south in Bolivia (12–17), which cluster together.

We did not include material from the eastern and southeastern margins of the range of *O. nitidus* (Brazil, Paraguay, and northeastern Argentina) in multivariate analyses because so few specimens were available. Those marginal localities are closest to the geographic distribution of *O. russatus*; for example, there are only three from Brazil (localities 142–144 in gazetteer for *O. nitidus* and map in fig. 79), two from Paraguay (localities 145 and 146), and one from nearby Provincia de Misiones in Argentina (locality 147). Specimens from Paraguay had been identified as "*O. intermedius*" by Myers (1982) and those from Misiones as "*O. capito intermedius*" by Massoia (1974), and subsequently listed as "*O. megacephalus intermedius*" by Chebez and Massoia (1996). We initially determined the three Brazilian specimens to be *O. nitidus*, as judged qualitatively from their size and pelage traits. To us, the Paraguay and Argentina samples also are examples of *O. nitidus*. In qualitative external and cranial features, they are closely similar to specimens collected from western Amazonia along the Andean foothills and adjacent lowlands. All have smaller crania and shorter molar rows than are typical of *O. russatus*. An a posteriori discriminant function classification of each of the specimens from these marginal sites in Brazil, Paraguay, and Argentina nestled their scores within the cluster of specimen scores representing *O. nitidus* in the canonical variate plots.

We have not examined Massoia's (1974) specimens from northeastern Argentina (Provincia de Misiones) that he identified as *intermedius*, but we suspect they are actually examples of *O. nitidus*. Massoia compared the two Misiones rats with seven "*O. legatus*" from Provincia de Salta. Cranial and dental measurements of his Salta sample have appreciably greater values than do the Misiones specimens, especially regarding interorbital breadth, breadth across the zygomatic plate, and length of toothrow. The exception is length of incisive foramina, which is much longer in the Misiones sample. These are the kind and magnitude of differences we observed in our samples: *legatus* has a much larger and more robust cranium than does *O. nitidus*, but has shorter incisive foramina, both absolutely and relative to occipitonasal length (see above where we contrast samples of Bolivian *legatus* and *O. nitidus*).

ORYZOMYS MACCONNELLI
Thomas, 1910

Oryzomys macconnelli was described by Thomas (1910: 186) and is based on an old adult female (BM 10.5.4.34; skull is shown in fig. 132 and measurements are listed in table 49) collected along the Supenaam River in northern Guyana (locality 9 in gazetteer) and donated to the British Museum by F. V. McConnell.

The new species, wrote Thomas (1910: 186–187), ''is readily distinguished from any of its allies by its rich rufous colour. It is probably a Guianan representative of the Brazilian *O. intermedius* Leche, but is more brightly coloured.'' He described *Oryzomys macconnelli* this way:

> Size comparatively large. Fur rich and sleek; hairs of back about 12 mm. in length. General colour above bright rich tawny or tawny ochraceous, darkened along the middle area of the back. Sides clearer ''tawny ochraceous.'' Under surface sharply defined white, the basal halves of the hairs slaty. Head rather browner than back. Ears large, blackish brown. Hands and feet silvery white. Tail long, very finely scaled, short-haired, brown above, dull white below.
>
> Skull somewhat like that of *O. intermedius*. General outline long and slender. Interorbital ridges well marked, evenly divergent, but little overhanging. Palatal foramina of medium length, slightly longer than the molar series.

Thomas's species was redescribed in 1913 by Allen as *Oryzomys incertus*, which was subsequently replaced by *Oryzomys mureliae* (Allen, 1915: 630) because the name *incertus* was already proposed. These are the only two names ever correctly associated with *O. macconnelli* (Tate, 1939: 189; Musser and Carleton, 1993: 723); their identity with *O. macconnelli* is discussed in Taxonomic Summary.

Although Hershkovitz (1960) treated *macconnelli* as a synonym, most other workers, before and after his footnote was published, recognized the taxon as a species distinct from *O.* ''*capito*'' (Gyldenstolpe, 1932; Tate, 1939; Ellerman, 1941; Cabrera, 1961; Carvalho and Toccheton, 1969; Pine, 1973; Gardner and Patton, 1976; Husson, 1973, 1978).

DISTRIBUTION AND HABITAT

The geographic distribution of *O. macconnelli*, as estimated by specimens examined, extends from the lowlands of southern Colombia east of the Andes south through Ecuador to southern Perú, and east through southern Venezuela (also see Ochoa et al., 1993), the Guiana Region, and that portion of Brazil within the Amazon Basin—from Amazonas in the west to the Belém area in the east (fig. 78). This broad area is congruent with what has been described as ''Amazonia,'' a region that Haffer (1987a: 111) defined as ''the Amazon Basin as well as the Guianas and southern to eastern Venezuela (southern part of the Orinoco drainage).'' Compare our map of Amazonia in figure 15 with the distribution of collection records for *O. macconnelli* in figure 78.

Both *O. macconnelli* and *O. yunganus* are restricted to Amazonia, as judged from collection records, but the latter has a more extensive range (fig. 14) and has been found in gallery forests through the cerrado. Collection records for *O. macconnelli* are in the heart of the tropical humid forest distribution; apparently, the species has not been collected in the evergreen riverine forest that threads its way through palm savanna and cerrado habitats.

Elevational records for *O. macconnelli* extend from near sea level in the Guiana Region and eastern portions of the Amazon Basin to 1524 m on Cerro de la Neblina in Venezuela and 915–1524 m along the foothills of the Andes in Perú. Vivar and Arana-Cardó (1994) trapped one *Oryzomys* they identified as *macconnelli* at Falso Paquisha (Cordillera del Cóndor, Río Comaina, Amazonas, Perú) at 900 m and considered it a new elevational record for the species, not realizing collection records existed for even higher elevations (see localities for Perú in gazetteer).

Information from specimen labels, field journals, and conversations with collectors suggests that *O. macconnelli* is restricted to primary tropical evergreen rain forest habitats, unlike the other Amazonian species *O. yunganus* and *O. megacephalus*, both of which occur throughout a habitat spectrum extending from primary rain forest through second-growth formations to shrubby clearings and abandoned agricultural fields in the forest. Below we summarize, by country, habitat descriptions associated with specimens of *O. macconnelli*.

French Guiana: We have information only for the specimens collected in the Arataye region at **Saut Pararé** (locality 1), the ''Ecological Station of the Museum National d'Histoire Naturelle'' (Dubost, 1988: 108). Voss and Emmons (1996: 95) summarized the published vegetational and climatological data for the area:

> Crique Arataye, a tributary of the Approuague, drains a large and virtually uninhabited black-water catchment in the lowlands of east-central French Guiana. Saut Pararé is in pristine evergreen forest far removed from resident human populations. . . . Fifteen years of weather records from Régina (about 70 km NE of Saut Pararé) document an average annual rainfall of 3700 mm. . . . The forest understory is very open and the canopy has an average height of about 30 m, with occasional emergents to 40 m. . . . The locally dominant families of trees are Burseraceae, Chrysobalanaceae, Lecythidaceae, and Mimosaceae. . . .

Venezuela: Specimens from **San Ignacio de Yuruaní** (locality 11) were obtained in 1986 and 1987 by R. S. Voss and his colleagues. Voss (field journal, AMNH, Mammalogy) noted that ''a mosaic of four major vegetation formations'' occurs in the region of San Ignacio de Yuruaní: savanna (''the most extensive habitat around San Ignacio, the term here used to include a continuum of grass- and/or sedge-dominated open plant formations''), morichales (''stands of moriche palm'' that are ''invariably surrounded by savanna''), arbustales (''scrublands whose vegetation grows on the weathered soils of exposed sandstone outcrops''), and broadleaf evergreen rain forest. Next to savanna, Voss wrote, evergreen rain forest is the most extensive formation,

> occurring as galleries of varying width along rivers or as large blocks of continuous growth. The forest canopy ranges in height from 15 m or so in secondary successional situations to 25 m or more in mature stands. Many larger trees are buttressed and woody lianas are abundant. Logs and tree trunks are sparsely mossy, the latter to 2 m or more above the ground. Epiphytes (orchids, bromeliads and ferns) are common but not really conspicuous. Palms, often stilted, are abundant in the understory and diffuse subcanopy, but none are canopy emergents; tree-ferns are also scattered through the understory. The undergrowth is generally sparse in mature stands but may be quite impenetrable in early successional growth; in the latter situations (chiefly tree-falls of varying age, and abandoned slash-and-burn plots), a stilt-rooted species of *Cecropia* typically forms a fairly open canopy above a dense and tangled growth of bamboos, gingers, *Heliconia*, seedling palms, shrubs and tall, stalked aroids. The clayey, reddish topsoil in the forest is thinly overlain by a layer of wet leaves, but there is no true humus layer.

All examples of *O. macconnelli* from San Ignacio de Yuruaní came from this evergreen forest (Voss and Emmons, 1996: figs. 15–17, provided photographs of rainforest habitats at this locality). Voss's notations accompanying the specimens documented the following local capture environments: ''in wet leaf litter or ground under logs in tall forest with sparse understory,'' ''on ground under elevated roots of *Cercropia* at edge of forest clearing with dense bamboo,'' ''at base of tree in forest with dense undergrowth of bamboo, aroids, *Heliconia*, shrubs, ferns and seeding palms,'' ''on ground in wet trash under shrubby palm in forest,'' and ''on the ground beneath dense undergrowth of Heliconias and shrubs in forest.''

The large series of *O. macconnelli* from **Auyán Tepuy** (locality 13) were collected along the base of the tepui at 1100 m and in the adjacent Camarata Valley at 460 m by G.H.H. Tate and J. A. Dillon. In both places tall tropical evergreen rain forest was interrupted by extensive savanna, and specimens were collected only in the forest (see figs. 2 and 4 showing the 1100 m camp and Camarata Valley camp in Tate, 1938).

One *O. macconnelli* was collected at **Cabecera del Caño Culebra** (locality 14), which is, wrote Handley (1976: 65), on ''Uninhabited, trailless, and undisturbed Cerro Duida Plateau'' where specimens were caught in ''island of high (12–20 m, occasionally 35 m) evergreen forest with slender trunks and branches mostly near tops, superficially similar to lowland forest of Cunucunuma Valley. Holdridge classification: LOWER MONTANE rain forest (bp-MB).''

Perú: Most specimens from **Teniente López** (locality 25) were collected 1.5 km north of the Teniente López in a ''Study Zone'' that is ''Rolling terrain (310–340 m) with steep slopes and small, sandy bottomed streams in primary rain forest'' (Duellman and Mendelson, 1995: 335).

Alfred L. Gardner collected the only example of *macconnelli* from **Balta** (locality 30). It was taken in a trap set at the base of a canopy tree in a narrow band of primary forest extending along a stream. Old second growth (largest trees 15–18 inches in diameter at breast height) was adjacent to the primary forest.

On the specimen label of an example from **Perené** (locality 34) collected by P. O. Simons in 1900 is the notation ‘‘in deep woods.’’

SYMPATRY

Among species in the former *O.* ‘‘*capito*’’ complex, the geographic range of *O. macconnelli* broadly overlaps those of *O. yunganus* and *O. megacephalus*, both of which also occur in the tropical evergreen rain forests of Amazonia. Examples of all three have been captured together at several localities (documented in appendix G).

Geographic distributions of *O. macconnelli* and *O. nitidus*, both members of the *O. nitidus* group, are also partially sympatric in western Amazonia. However, examples of the two species have been collected together only at one site in Perú (Balta, locality 30 in gazetteer for *O. macconnelli*); we have already discussed this co-occurrence in the section on sympatry in the account of *O. nitidus*. The only other record of sympatry within the group is that between *O. macconnelli* and the species represented by the sample from central Pará (which we describe in the following account); specimens of each were collected at locality 50 (see gazetteer for *O. macconnelli*).

The other members of the former *O.* ‘‘*capito*’’ complex have geographic ranges allopatric to that of *O. macconnelli* (judged from documented specimens): *O. russatus* in southeastern Brazil, southern Bolivia, and northern Argentina; *O. bolivaris* and *O. talamancae* in the trans-Andean region west and north of Amazonia.

DESCRIPTION OF THE SPECIES

Until 1976, *Oryzomys macconnelli* had only been recorded from Colombia, Venezuela, the Guianas, and Brazil. Gardner and Patton (1976: 40) provided the first record from Perú and noted the species’ distinctive features:

> We have identified the 2*n* = 64, FN = 64, long-haired, reddish *Oryzomys* from eastern Perú as *O. macconnelli*. . . . This species is characterized as follows: long and lax, dark reddish brown dorsal pelage; large incisive foramina, widest in the middle and tapering anteriorly and posteriorly; palatal excrescences obsolete; sphenopalatine pits compound; cheek teeth comparatively simple; second upper molars with short first and second primary folds, and with a shallow enamel island between the first primary and major folds (first internal fold discrete, but lost early in wear); and third upper molars with persistent first internal fold and comparatively well-developed major fold.

Gardner and Patton, as well as Thomas before them, accurately described *Oryzomys macconnelli*. This handsome rat (fig. 102) is moderately large in body size with a tail equal to or conspicuously longer than length of head and body (table 37). Prime adult dorsal fur exhibited by most individuals is lustrous tawny or reddish brown that is even brighter along sides of the head and body, an ochraceous tawny as Thomas noted. The entire dorsum is bright and without pattern in some specimens, but others are darker through the middorsal region of back and rump. A very few animals have uniform, grizzled, dark tawny upperparts. The long (11–15 mm over the back and rump) and lax fur is soft to the touch. Underparts of most specimens are bright, whitish gray; others are darker because the white portions at the tips of the hairs are shorter and more of the gray at the bases of the hairs shows through. Some specimens have a an all-white patch on the throat or pectoral region. Ears are brown with inner and outer surfaces sparsely covered with short, fine, and buffy hairs. The longest mystacial vibrissae, when appressed against the study skin, reach the posterior margin of the pinnae but do not extend beyond it. The tail is sparsely haired and appears bicolored, its dorsal surface is brown, and the ventral surface is unpigmented for about two-thirds of its length; the distal one-third or one-fourth is either pale brown or the same tone as the upper surface. Hind feet are long and narrow and their plantar surfaces bear six pads. Lengths of the digits relative to one another and to the metatarsus closely resemble the proportions shown for *O. yun-*

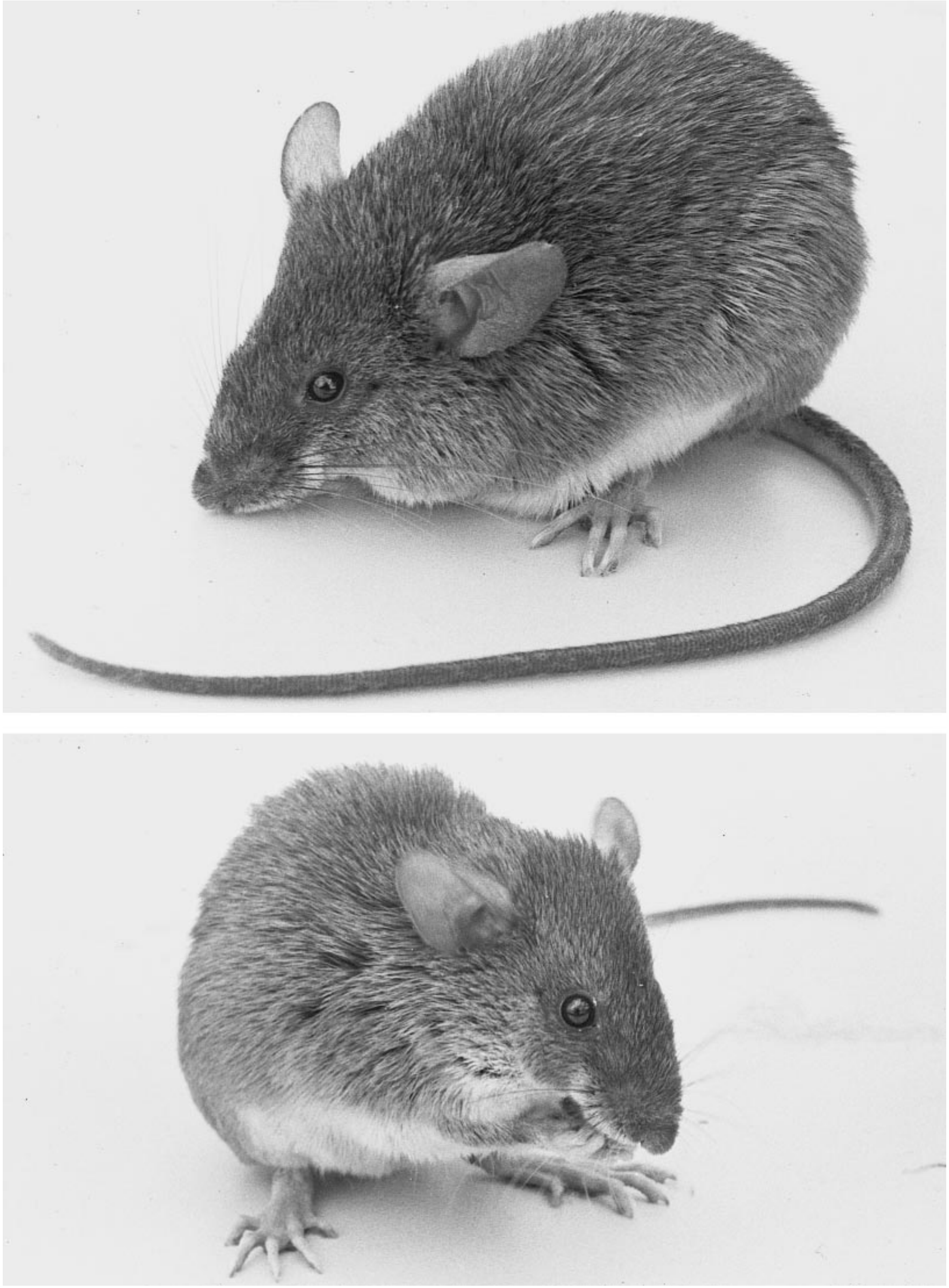

Fig. 102. An adult male *Oryzomys macconnelli* (USNM 448585) from San Ignacio de Yuruaní, Estado de Bolívar, Venezuela, collected June 19, 1986. We are grateful to R. S. Voss for providing us with these prints.

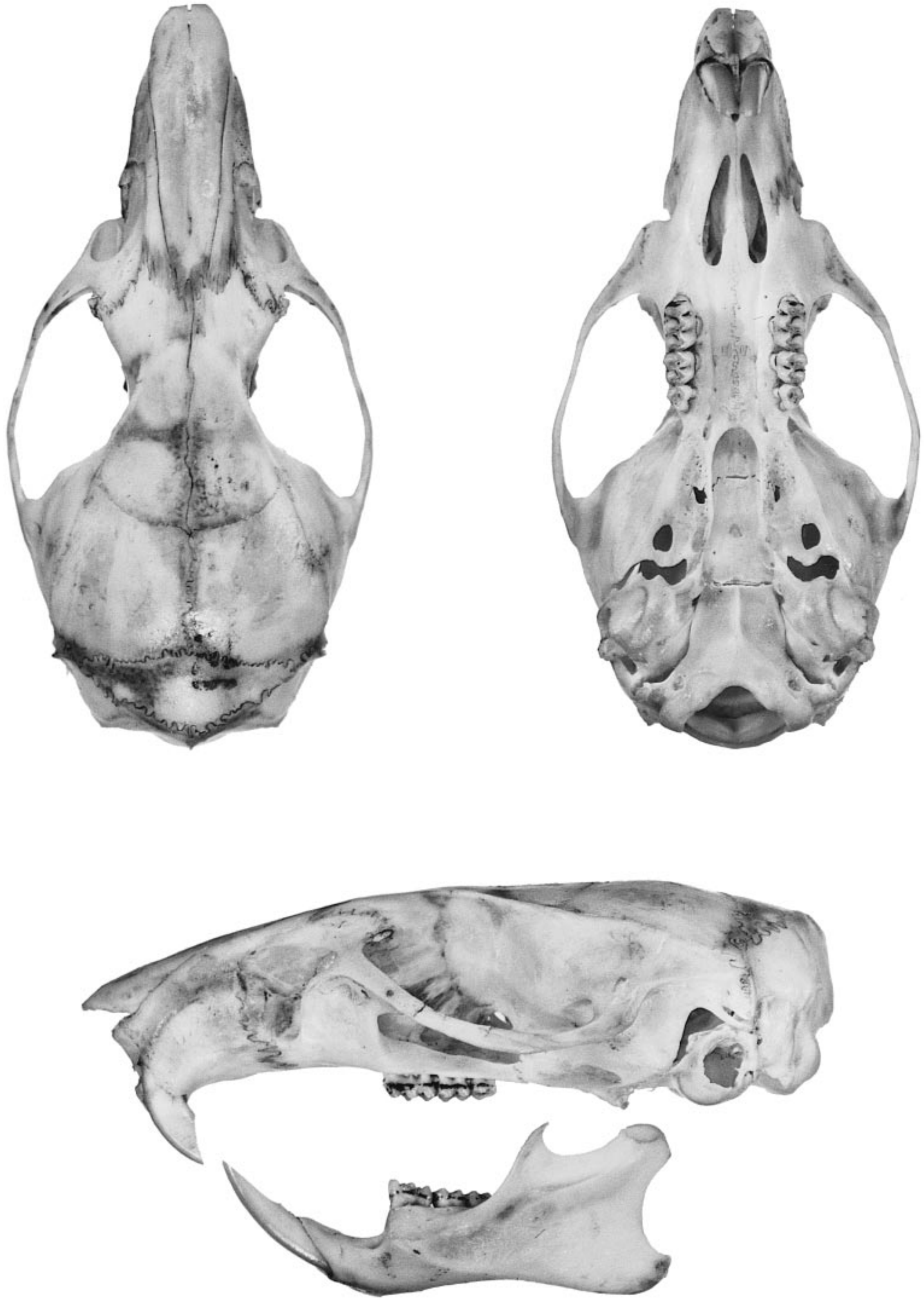

Fig. 103. Cranium and dentary of an adult *Oryzomys macconnelli* (AMNH 130961) from Auyán Tepuy, Departamento de Bolívar, Venezuela. ×3.

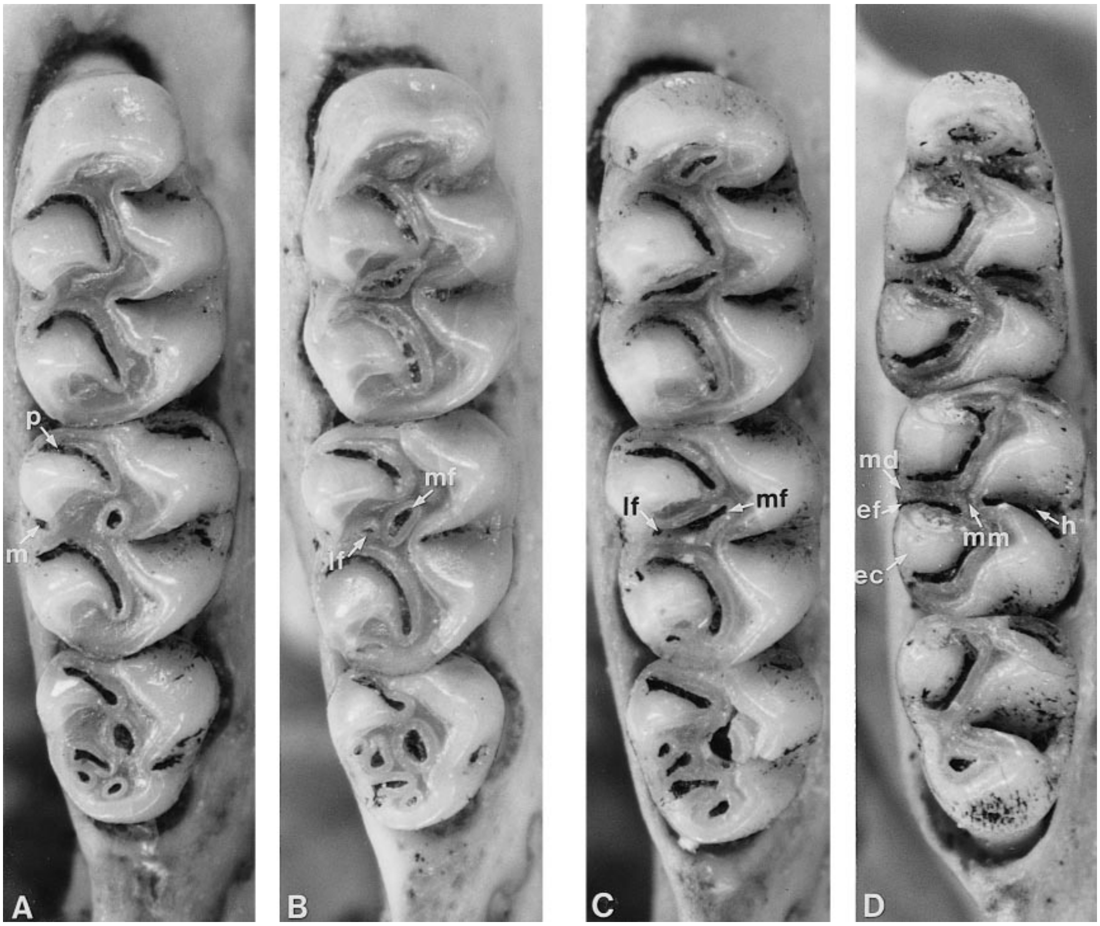

Fig. 104. Views of molar rows portraying variation in occlusal patterns due to wear in examples of *O. macconnelli* from Boca del Río Curaray, Departamento de Loreto, Perú. **A**, Right upper molars (AMNH 71579), adult; **B**, right upper molars (AMNH 71580), adult; **C** and **D**, right upper and lower molars (AMNH 71586), juvenile–young adult (half of body still in juvenile pelage). The second upper molars in all three have a short paraflexus (**p**) and a shallow mesoflexus (**m**). A medial fossette (**mf**) is present in **A**, but the labial fossette (**lf**) is nearly obliterated. Many specimens of *O. macconnelli* exhibit this pattern and seem to have only one fossette; in these animals, the fossette present is always the medial, not the labial. Large medial and very small labial fossettes are present on the second molar of **B**; the labial fossette would have been obliterated had the rat lived long enough for the molar surfaces to have become more worn. This configuration—a large medial fossette and a much smaller labial one—is typically found in examples of *O. macconnelli* with slightly to moderately worn occlusal surfaces. Medial and labial fossettes are confluent in the young rat (**C**), a pattern less commonly encountered in samples. In the second lower molar (**D**), the hypoflexid (**h**) extends only halfway across the tooth and is separated from its lingual counterpart, the entoflexid (**ef**), by a short median murid (**mm**). In some specimens, the lingual margins of the mesolophid (**md**) and entoconid (**ec**) have fused, thereby transforming the entoflexid into a shallow lingual crease and an elongate fossettid. ×20. See also figures 29–32.

ganus and *O. megacephalus* in figure 17. Dorsal surfaces of front and hind feet are densely covered by silvery white hairs, so feet appear solid white (unless stained by grease in dry museum specimens). Each claw is nearly hidden by a sheath of silvery white hairs that extends well beyond the claw tip.

In general outline, the cranium of *O. mac-*

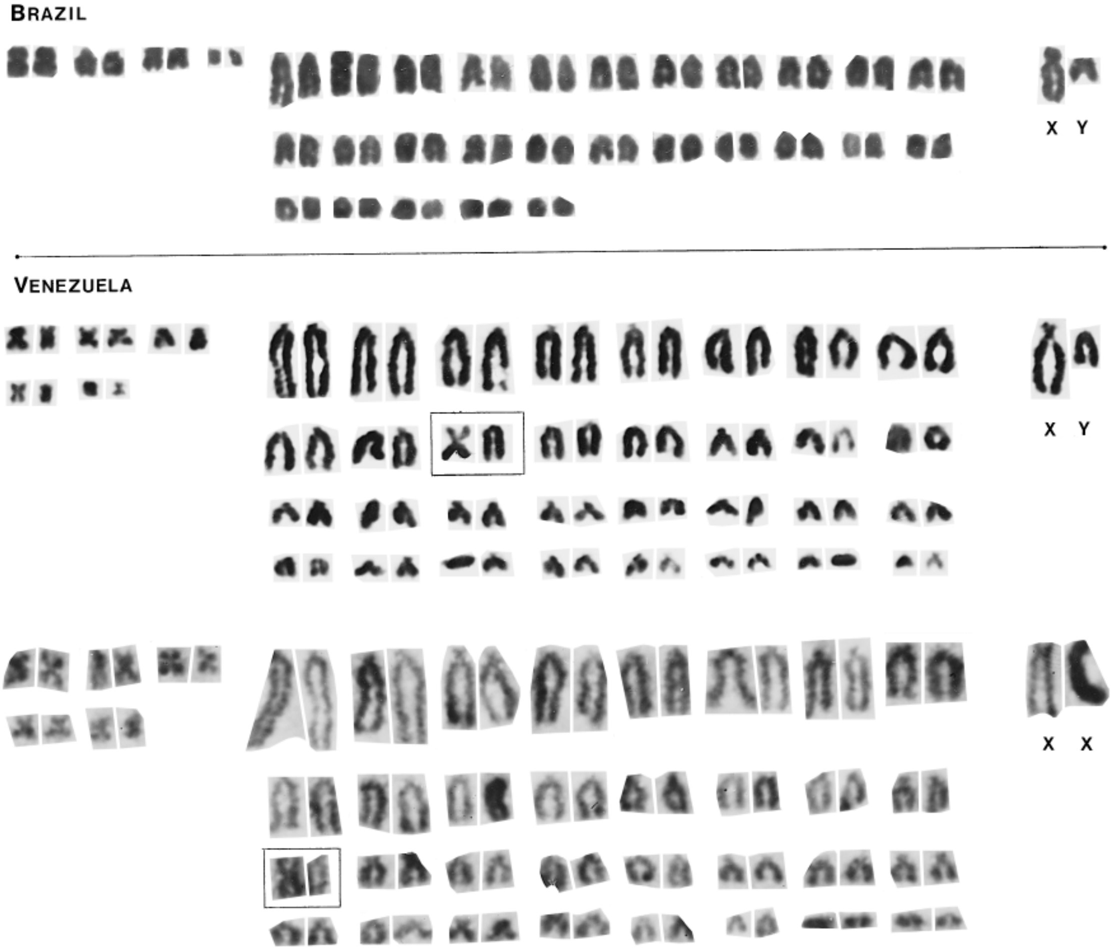

Fig. 105. Karyotypes from examples of *Oryzomys macconnelli* obtained in Brazil and Venezuela. The Brazilian sample ($2n = 64$, FN = 70) is derived from a female (JUR 386) collected at Lago Vai-Quem-Quer, right bank of Rio Juruá (03°19′S/66°01′W), Estado do Amazonas, Brazil. The male (USNM 448585) and female (MHNLS 8060) from Venezuela were captured at San Ignacio de Yuruaní in Estado de Bolívar (locality 11 in gazetteer). Both specimens are characterized by $2n = 76$ and FN = 85 (or higher as explained in text). Boxes enclose the metacentric and acrocentric unpaired autosomes that we arbitrarily matched. See text for discussion.

connelli is long and slender (fig. 103); as Thomas noted, its shape is not unlike those of the other species in the *O. nitidus* group, *O. nitidus* and *O. russatus* (figs. 80, 112). All three species share an elongated rostrum, a moderately wide interorbit and braincase, small auditory bullae, and a primitive carotid circulatory pattern (sphenofrontal foramina, squamosoalisphenoid grooves, stapedial foramina, and grooves for infraorbital branch of stapedial artery are all evident on each cranium; figs. 27, 151). *Oryzomys macconnelli* has short incisive foramina (that in outline resemble a teardrop), a long bony palatal bridge, a narrow zygomatic plate, moderately conspicuous ridges or shelves outlining dorsolateral margins of a wide interorbit, and it generally lacks alisphenoid struts (table 38); this combination is distinctive for the species. Each dentary is somewhat elongate (fig. 103) and has a small coronoid projection.

Like all the other species in the former *O.* ‘‘*capito*’’ complex, the upper incisors of *O. macconnelli* are opisthodont in configuration relative to the rostrum. Their enamel layers, as well as those of the lowers, are yellow-orange or deep orange. Molars are tuberculate and brachydont with two rows of cusps arranged in opposing labial–lingual pairs (fig. 104). Occlusal arrangement of cusps and folds are not distinctively different from the other species described and contrasted here in this report (see, for example, figs. 30 and 32 where patterns are contrasted among *O. yunganus*, *O. macconnelli*, *O. nitidus*, and *O. megacephalus*). Second upper molars have both a labial and a medial fossette (enamel island, as described by Gardner and Patton, 1976); second lower molars usually show a fossettid and always have a short hypoflexid.

Chromosomal samples of populations from Brazil and Venezuela are now available that differ from the karyotype ($2n$ = 64, FN = 64) reported by Gardner and Patton (1976) for specimens from eastern Perú (Balta, locality 30 in gazetteer for *O. macconnelli*). A $2n$ of 64 and a FN of 70 (fig. 105) was obtained by J. L. Patton and coworkers for populations from western Brazil and karyotype with a $2n$ of 76 and a FN of 85 (fig. 105) by R. S. Voss and colleagues from Estado de Bolívar, Venezuela (San Ignacio de Yuruaní, locality 11). The chromosomal preparation of the Peruvian sample reported on by Gardner and Patton (1976) was not good enough to permit the clear identification of all chromosomes. Nevertheless, they described the karyotype as consisting of 1 pair of small metacentrics, 31 pairs of acrocentrics graded from large to small, and acrocentric X chromosomes of undetermined size (the only specimen karyotyped was a female). The autosomes of the Brazilian sample consist of 4 pairs of medium-sized to small metacentrics and submetacentrics, 27 pairs of acrocentrics graded from large to small, and a large subtelocentric and a small acrocentric Y chromosome (fig. 105, table 13). The karyotype of the Peruvian specimen has the same diploid number, but because the Brazilian animals have four pairs of biarmed autosomes instead of the single pair reported for the Peruvian animal, the fundamental number is 70, not 64. Additional preparations from Peruvian specimens may show the reported differences to be an artifact of the poor quality of original chromosomal slides.

The autosomes of the Venezuelan *O. macconnelli* (MHNLS 8060, female; USNM 448585, male) consist of 5 pairs of small metacentrics and submetacentrics, 31 pairs of acrocentrics graded from large to small, and 2 unpaired chromosomes (a medium-sized metacentric and a medium-sized acrocentric, hence the odd-numbered FN of 85). The sex chromosomes consist of a large subtelocentric X and a small acrocentric Y, both of which resemble the X and Y chromosomes of the Brazilian samples (fig. 105). Several pairs of the acrocentric autosomes bear discernible second arms and could be classed as biarmed chromosome, thus raising the FN to as high as 107. In contrast to the Brazilian *O. macconnelli*, the Venezuelan karyotype has 5 pairs (instead of 4) of small metacentrics and submetacentrics and 31 pairs (instead of 27) of acrocentric autosomes (compare karyotypes in figure 105). We have arbitrarily paired the unmatched medium-sized metacentric autosome with an acrocentric of comparable total arm length. While possibly linked to the sex chromosome system, this unpaired element is not the Y chromosome because we also found it in metaphase spreads of the female.

GEOGRAPHIC VARIATION

Geographic relationships among the population samples of *O. macconnelli* (table 39), as derived from mean values of cranial and dental measurements, are summarized by the cluster diagram in figure 106. Samples from the Guiana Region (the Guianas, eastern Venezuela, and Estado do Amapá in Brazil, samples 1, 2, and 8, respectively), all north of the Amazon River in eastern Amazonia, are associated apart from those from south of the river in western and eastern portions of Estado de Pará, Brazil (samples 6 and 7), and from western reaches of Amazonia in Ecuador, Perú, and adjacent Brazil (samples 3–5).

Our study of geographic variation is based solely on morphometric traits, for we could not detect any significant variation from place to place in features associated with the skins. Tone of dorsal fur, for example, may be predominantly bright in one sample and more somber in another, but in any sufficiently large series, such as the one from Auyán

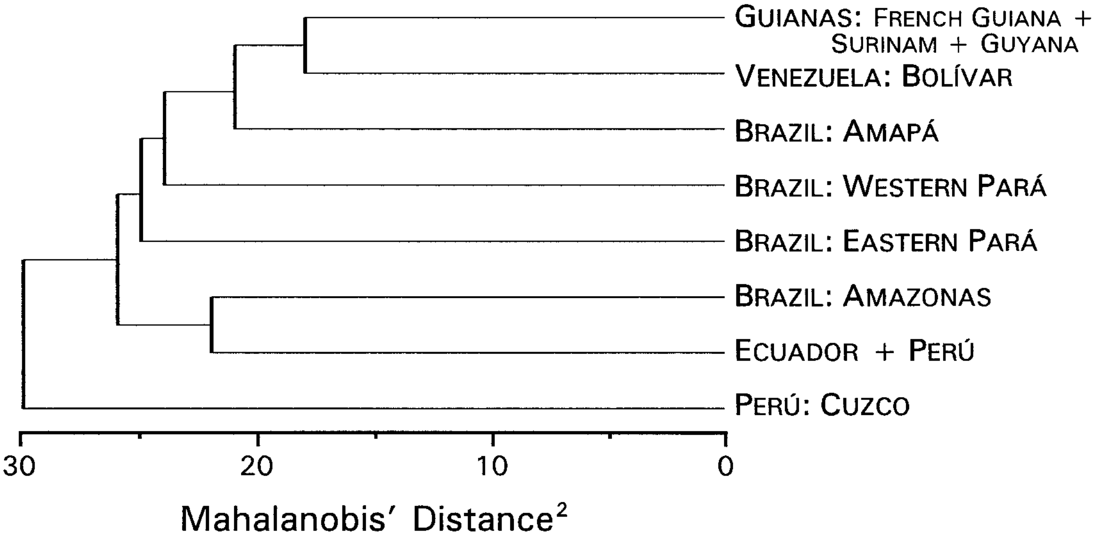

Fig. 106. UPGMA clustering of eight population samples of *Oryzomys macconnelli* (samples 1–8) generated from Mahalanobis' distances (D^2) among group centroids. Geographic origin and size of samples are indicated in table 39, mean values of measurements for variables are listed in appendix E, specimens measured are identified in appendix F. See discussion in text.

Tepuy, the complete range from bright to somber pelage exists.

THE PARÁ SAMPLE

Originally misidentified first as *O. macconnelli* and then as *O. nitidus*, the 17 examples from three collection localities in central Estado de Pará, Brazil, actually represent a distinct species that we name and describe as:

Oryzomys emmonsae, new species

HOLOTYPE: MZUSP 27150, an old adult male captured by L. H. Emmons (original number 559) on September 3, 1986 from east bank of Rio Xingu, 52 km SSW Altamira (03°39′S/52°22′W; locality 148 on map in fig. 79), below 100 m in Estado de Pará, Brazil. The specimen consists of a stuffed museum skin with accompanying cranium and mandible; all elements are well preserved and intact. Samples for chromosomal and biochemical analyses were extracted from the specimen; microscope slides with chromosomal spreads are stored at USNM and tissues are at MVZ. External, cranial, and dental measurements of the holotype are listed in table 49.

REFERRED SPECIMENS: Sixteen other specimens from lowlands below 200 m in Estado de Pará (localities 148–150 in gazetteer and map in fig. 79): two additional examples collected by L. H. Emmons at the type locality, USNM 549551 (August 22, 1986) and USNM 549552 (August 26, 1986); USNM 543327–543338 from Marabá, Serra Norte (06°00′S/50°20′W); USNM 519775 and 521530 from 73 km N and 45 km W Marabá, near Pôrto Jatobal (04°41′S/49°32′W). All specimens are preserved as museum skins with crania and mandibles; chromosomal spreads were obtained from the holotype (stored at USNM) and biopsy tissue was also saved from the holotype and USNM 549552 (stored at MVZ).

DIAGNOSIS: A species in the *Oryzomys nitidus* group resembling *O. nitidus* in its pelage and skin coloration as well as gross chromosomal composition, but characterized by longer tail relative to head and body; the cranium is small and delicate, which reflects a long but slender rostrum, narrow zygomatic plates, narrow interorbit with smooth dorsolateral margins, and narrow occiput; the incisive foramina are short and wide, and the bony palate correspondingly long.

DESCRIPTION: *Oryzomys emmonsae* is moderately large in body size with a tail appreciably longer than length of head and body (table 37). The dorsal coat is moderately long (8–10 mm over back and rump), soft, and bright tawny brown highlighted by ochraceous tones along sides of head and body. The head is slightly darker due to a greater concentration of black-tipped hairs. The eyes are outlined by dark brown lids, but not encircled by a wider ring or mask. Ears are dark brown and covered with fine buffy brown hairs over inner and outer surfaces. The longest of the facial vibrissae extend only slightly beyond the ear when laid back against the head. Underparts of head and body are white and lightly suffused with gray; the long white tips of the overhairs nearly mask their gray bases. Ten of fifteen specimens show a small to large white chest patch in which the hairs are unpigmented to their bases. The long tail is bicolored, tawny brown above and unpigmented below for most of its length, except the last 10 mm, which is brown. Dorsal surfaces of front and hind feet are unpigmented and densely covered with white hairs. Palmar and plantar surfaces are brown. Six plantar pads adorn the surface; the hypothenar is small and inconspicuous, the others prominent. Dense ungual tufts extend beyond and nearly conceal the claws. Proportions of the hind digits relative to the metatarsal region are similar to the configurations illustrated for *O. megacephalus* and *O. yunganus* (fig. 17).

The cranium is elongate and delicate (fig. 107), an impression conveyed by its moderately long and slender rostrum, narrow interorbit with smooth dorsolateral margins and concave sides, gracile zygomatic arches, narrow zygomatic plates with correspondingly shallow notches, and narrow occipital region. The incisive foramina are moderately wide and short, the bony palate is long, and the roof of the mesopterygoid fossa is complete. A sphenofrontal foramen, squamosoalisphenoid groove, large stapedial foramen, and groove on the ventral surface of the pterygoid plate indicate the cephalic arterial circulation to be like the complete pattern found in all the other species in the *O. nitidus* group (see fig. 151 and table 52).

Form of each dentary is similar to that in *O. nitidus* and *O. macconnelli*, but appears more gracile. The coronoid process is short and delicate, and the posterior margin deeply concave between condyloid and angular processes (fig. 107).

Configuration of the upper incisors relative to the rostrum, enamel pigmentation of upper and lower incisors, and molar occlusal patterns seen in *O. emmonsae* are similar to these traits as observed in *O. nitidus* (compare figs. 80 and 107).

The karyotype of *O. emmonsae* is derived from one specimen, the holotype, which has a $2n$ of 80 and a FN of 86 (fig. 109). The autosomes consist of 4 pairs of small metacentrics and submetacentrics and 35 pairs of large to small acrocentrics, the first pair of which is distinctly larger than the others. The sex chromosomes consist of a very large subtelocentric X and a small acrocentric Y. Some of the acrocentric autosomes have short second arms and could be classed as biarmed, but the FN is based on classifying them as uniarmed chromosomes. Other investigators might classify at least two of these pairs as biarmed, thereby raising the FN to 90. This karyotype closely resembles that reported for *O. nitidus* by Gardner and Patton (1976) from eastern Perú, and for *O.* ''*capito*'' (= *O. russatus*) by Almeida (1980, fide Maia, 1990) from Estado do São Paulo, Brazil.

COMPARISONS: In its morphological traits, *O. emmonsae* is most like *O. macconnelli* and *O. nitidus*; detailed comparisons were presented in the account of *O. nitidus* and we only summarize the contrasts here (see also figs. 84–90). Compared with samples of *O. macconnelli*, *O. emmonsae* has shorter and brighter pelage, the head and body averages shorter but the tail longer (so tail is even longer relative to length of head and body; table 37), and it weighs less (table 37); overall, the cranium is smaller and gracile (see descriptive statistics in appendix E), the occiput (lambdoidal breadth) narrower relative to zygomatic breadth, and the molar row shorter. The two species also differ in chromosomal complements (table 13). In *O. emmonsae*, breadth of zygomatic plate, length of bony palate, and shape of incisive foramina relative to other cranial dimensions are proportionally similar to samples of *O. macconnelli*

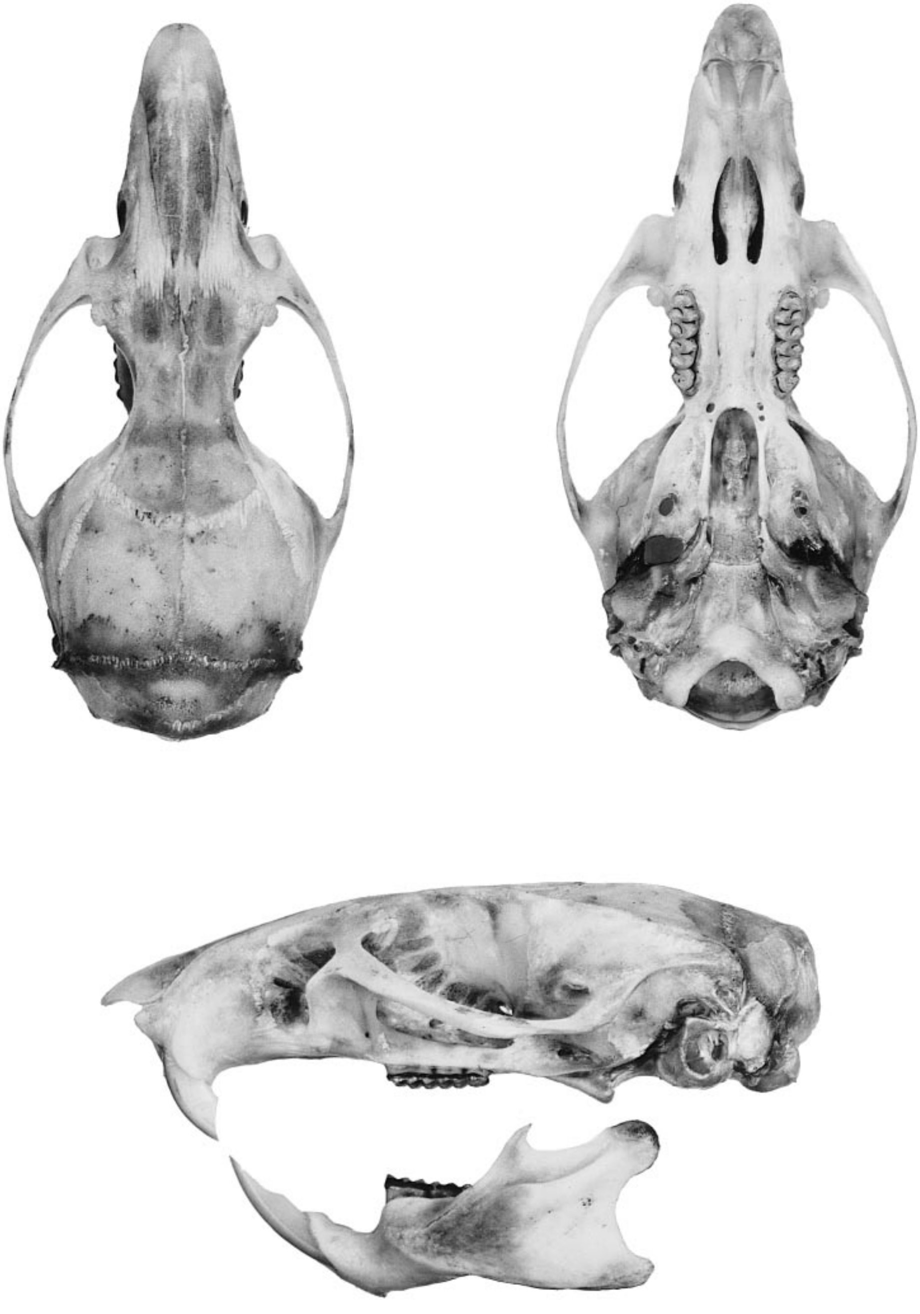

Fig. 107. Views of cranium and dentary of USNM 549552, one of the three examples of *Oryzomys emmonsae* captured at the type locality (east bank of Rio Xingu). ×2.

(fig. 84). Alisphenoid struts are uncommon in samples of both species (table 38).

The series of *O. emmonsae* more closely resembles samples of *O. nitidus* in external traits, but the tail averages longer (table 37). The cranium of *O. emmonsae* is small and delicate compared with the large and robust skull of *O. nitidus* (appendix E, figs. 89 and

Fig. 108. Occlusal views of right upper and lower molar rows of *Oryzomys emmonsae* (USNM 543333, Marabá, Serra Norte, Estado de Pará, Brazil). ×20. Occlusal patterns closely resemble those of *O. nitidus* (see fig. 81). Also see figures 29–32.

90). Breadth of the interorbit and rostrum is proportionally like *O. nitidus* (*O. macconnelli* has a relatively wider interorbit and rostrum than either species; fig. 84), but dorsolateral margins of the interorbit are smooth and not bounded by low ridges (which is characteristic of *O. nitidus*). Other proportions of the cranium are unlike *O. nitidus* and resemble the configurations seen in samples of *O. macconnelli*: the zygomatic plate is much narrower relative to most other cranial dimensions, the bony palate is longer relative to occipitonasal length, and the incisive foramina are shorter and wider relative to nearly all other cranial dimensions (fig. 84). Alisphenoid struts rarely occur in available samples of *O. emmonsae* but are found in about half of all specimens of *O. nitidus* examined (table 38). Gross chromosomal traits are similar in *O. emmonsae* and *O. nitidus* (both exhibit 2*n* = 80 and FN = 86; table 13); other kinds of preparations (G-, C-, and R-bandings, for example) will be necessary to detect differences in karyotypes, if any exist.

DISTRIBUTION AND HABITAT: Specimens of *Oryzomys emmonsae* come from Amazonia south of the Amazon River between the lower portions of the Xingu and Tocantins rivers. Geographic boundaries of *O. emmonsae* are unknown, but its absence from the well-collected vicinity of Belém may be significant.

Capture localities of *O. emmonsae* are in a region mapped as Amazonian tropical evergreen rain forest (see, for example, the map in Hueck and Seibert, 1981). The only information we have about habitat at any specific locality is in a summary report prepared by members of the field crew who worked at the type locality. Voss and Emmons (1996: 101) abstracted relevant portions from that account, which included this description of forest habitats (also see fig. 110):

> The dominant vegetation in the area surveyed can be categorized as tropical evergreen rainforest. Within this broad formation, several more or less distinctive vegetational complexes were sampled; seasonally flooded forest (várzea) near the banks and on the islands; unflooded forest (terra firme) on upper, better drained slopes; palm swamps, both with and without a dense herbaceous understory; and viny forest, usually with close stands of bamboo. The distinctiveness of these plant associations and their intergradation seemed dependent on local edaphic factors and drainage patterns. . . .

All three examples of the new species from the Rio Xingu were collected by L. H. Emmons in the ‘‘viny forest’’ (Emmons, field catalog, USNM Mammalogy Archives)—in a ‘‘bamboo thicket on ground’’ (MZUSP 27150), a ‘‘viny bamboo thicket’’ on the ground (USNM 549551), and in ‘‘viny forest on ground under log’’ (USNM 549552).

Readers should consult Voss and Emmons (1996: 101–103) for a more expansive description of the survey site along the Rio Xingu and a list of the mammal species collected or observed during the period of fieldwork (*O. emmonsae* is identified as *O. nitidus* in that list).

SYMPATRY: Among members of the former

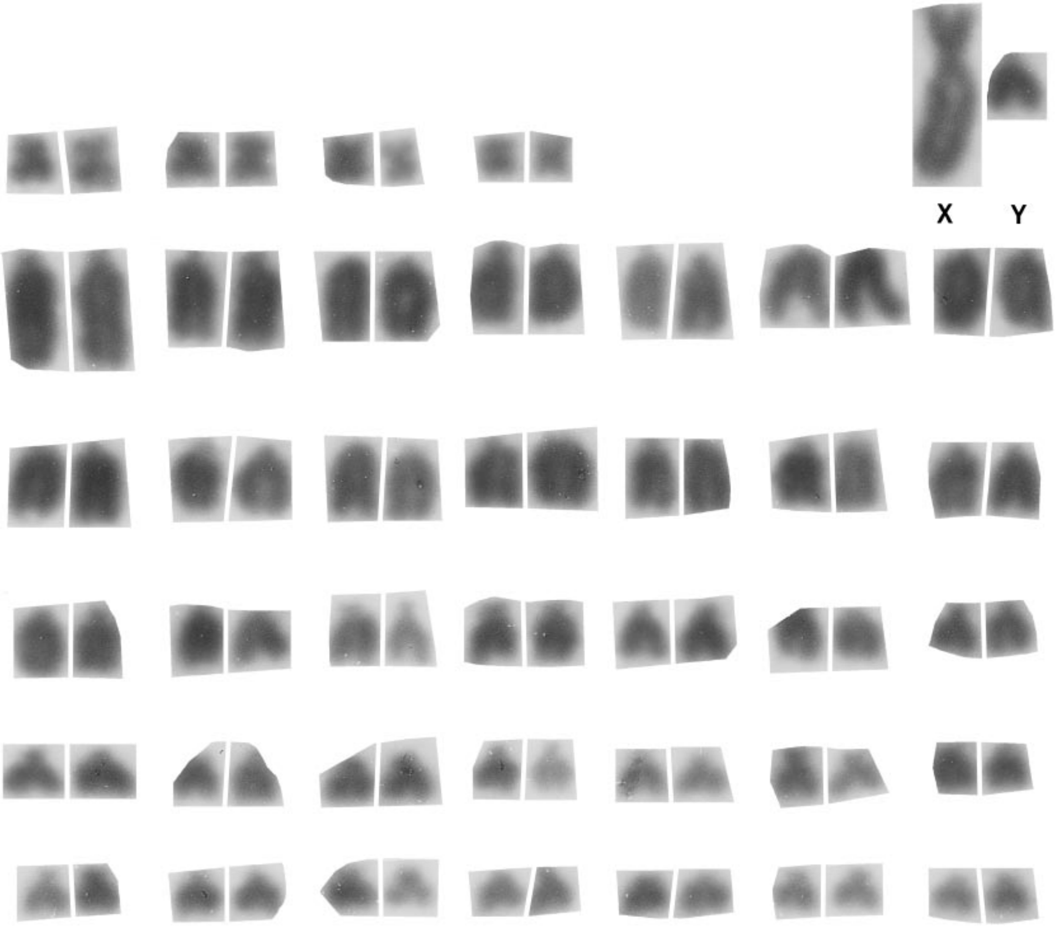

Fig. 109. Karyotype of male *Oryzomys emmonsae* (MZUSP 27150, the holotype), collected on the east bank of Rio Xingu, 52 km SSW Altamira, Estado de Pará, Brazil. Diploid number is 80, fundamental number is 86.

O. ''*capito*'' complex, the geographic distribution of *O. emmonsae* overlaps portions of the ranges of *O. megacephalus*, *O. yunganus*, and *O. macconnelli*, which, judged from specimens examined, are also primarily confined to Amazonia (see the accounts of those species). Examples of each species have been captured along with specimens of *O. emmonsae* in different combinations at the same place. A series of *O. megacephalus* (specimens in USNM and MZUSP) was taken at the type locality. The site at **73 km N and 45 km W Marabá** yielded examples of *O. emmonsae* and *O. macconnelli* (USNM 519772–519774, 519776, 521437). The documented range of *O. emmonsae* is distant from those recorded for *O. nitidus* and *O. russatus*, the other members, in addition to *O. macconnelli*, forming the *O. nitidus* group (see map in fig. 79).

REMARKS: The distribution shown by available examples of *Oryzomys emmonsae*—south of the Amazon River in the lower reaches of the basin—is unique not only among species in the former *O.* ''*capito*'' complex, but among all South American rainforest species of muroids with which we are familiar. The only documented exception might be *Oxymycterus amazonicus*, recently described by Hershkovitz (1994: 23) and represented by specimens ''from the south bank of the lower Rio Amazonas and lower parts

Fig. 110. Rio Xingu, 52 km SSW Altamira, Estado de Pará, Brazil. **Top**: Lowland tropical evergreen rain forest seen from the air. **Bottom**: View of campsite on edge of river. Examples of *Oryzomys emmonsae* were captured in this forest. Photographed by M. D. Carleton in 1986.

of tributaries Tocantins, Xingu, Tapajós, and middle Rio Madeira''; 9 of the 15 specimens examined by Hershkovitz were collected along the Rio Xingu near the type locality of *O. emmonsae*. However, we found the distribution of *O. amazonicus* to be much broader than Hershkovitz indicated and discordant with the range of *O. emmonsae* as we document it here.[8] *Oryzomys emmonsae* probably occurs over a greater area than we have indicated, and a better estimate of its actual distribution can be obtained by field surveys and sorting through specimens in museums where we have not worked (Brazilian institutions, for example).

The only habitat information about *Oryzomys emmonsae* comes from the three specimens captured at the type locality. All were trapped on the ground in ''viny forest'' (see above). Other kinds of forest habitats were also surveyed by members of the field team (Voss and Emmons, 1996: 101), but examples of *O. emmonsae* were not encountered. The association of ''viny forest'' and an *Oryzomys* with an appreciably long tail relative to length of head and body tempts us to speculate that *O. emmonsae* may be scansorial, active on substrates above ground as well as on the ground. The ratio of tail length relative to head and body approaches that of *O. subflavus* (table 37), which is terrestrial but also a good climber (Alho and Villela, 1984). This and other aspects of the biology of *O. emmonsae* remain to be learned.

ETYMOLOGY: Named for Dr. Louise H. Emmons (fig. 111), a Research Associate in the Division of Mammals at the National Museum of Natural History, Smithsonian Institution. She collected the holotype and two other specimens of the new species along the lower Rio Xingu, which is just one example of her survey efforts in tropical South America that have yielded extensive and significant contributions toward understanding mammalian diversity in the Neotropics.

ORYZOMYS RUSSATUS (Wagner, 1848)

Hesperomys russatus Wagner (1848) is the oldest available name we can identify for the species formerly known as *Oryzomys intermedius*. The names *physodes* (Brants, 1827: 139; preoccupied by *physodes* Olfers, 1818), *intermedia* (Leche, 1886: 693), *coronatus* (Winge, 1887: 51), *legatus* (Thomas, 1925: 577), and *kelloggi* (Ávila-Pires, 1959a: 2) apply to the same species; *moojeni* (Ávila-Pires, 1959b: 3) is probably also a synonym. Reasons for our allocations of these names are provided in Taxonomic Summary.

Wagner's (1848: 312) description of *Hesperomys russatus*, or ''Die goldfalbige Scharrmaus'' (gold-yellow Scharrmaus; translated literally, ''Scharrmaus'' is scrapemouse, but the meaning in German refers to a mouse with claws that scratches in the soil) is short and based only on external traits (translated by E. Brothers and checked by R. Hutterer; the original German is reproduced in appendix Q):

> The dorsum is vibrant golden pale orange flecked with a little black, somewhat lighter to the sides. The underside is sharply delineated and is a beautiful yellow-white, becoming paler at the neck and the medial surfaces of the hind legs. The feet have dirty white fur and the soles are bare. The ears have a hint of fine hairs; the tail is nearly hairless, pale, and darker on the dorsal surface.
>
> This Scharrmaus, brought back by Natterer from Ypanema, is so similar to *Mus physodes* Licht, that it is only by the vibrant coloration, the sparse yellow of the underside and snout-tip of the former, which is the only specimen known to exist in Berlin, that they appear to be distinguished. However, as they share

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[8] We have identified 89 examples of *Oxymycterus* from Brazil that exhibit the morphological characters described for *O. amazonicus* by Hershkovitz (1994) that were, with one exception, not examined by him. They are listed below.

Estado do Mato Grosso: Aripuanã (USNM 546005–546015, 546028–546055); Campos Novos, at southern edge of Serra do Norte (AMNH 37101).

Estado de Pará: Piquiatuba, right side of lower Rio Tapajós near Santarém (AMNH 94809); Tauari, on right bank of lower Rio Tapajós, 87 km SSW Santarém (AMNH 94802–94808, 94826); south of Santarém on BR 165, the road connecting Santarém with Cuiabá (USNM 544637–544640); Santarém, Mojui Dos Campos (USNM 546016–546027); 54 km S, 150 km W Altamira (USNM 519783–519786, 521481–521484, 521488, 521491, 521492, 521538); 18 km S, 19 km W Altamira (USNM 521485–521487, 521489, 521493–521496, 521536, 521537); 73 km N, 45 km W Maraba (USNM 519787, 521490).

Judged by these examples, *O. amazonicus* extends well south of the Amazon River into northwestern Mato Grosso, indicating a much more expansive distribution than indicated in the original description (Hershkovitz had borrowed one of the specimens from Aripuanã).

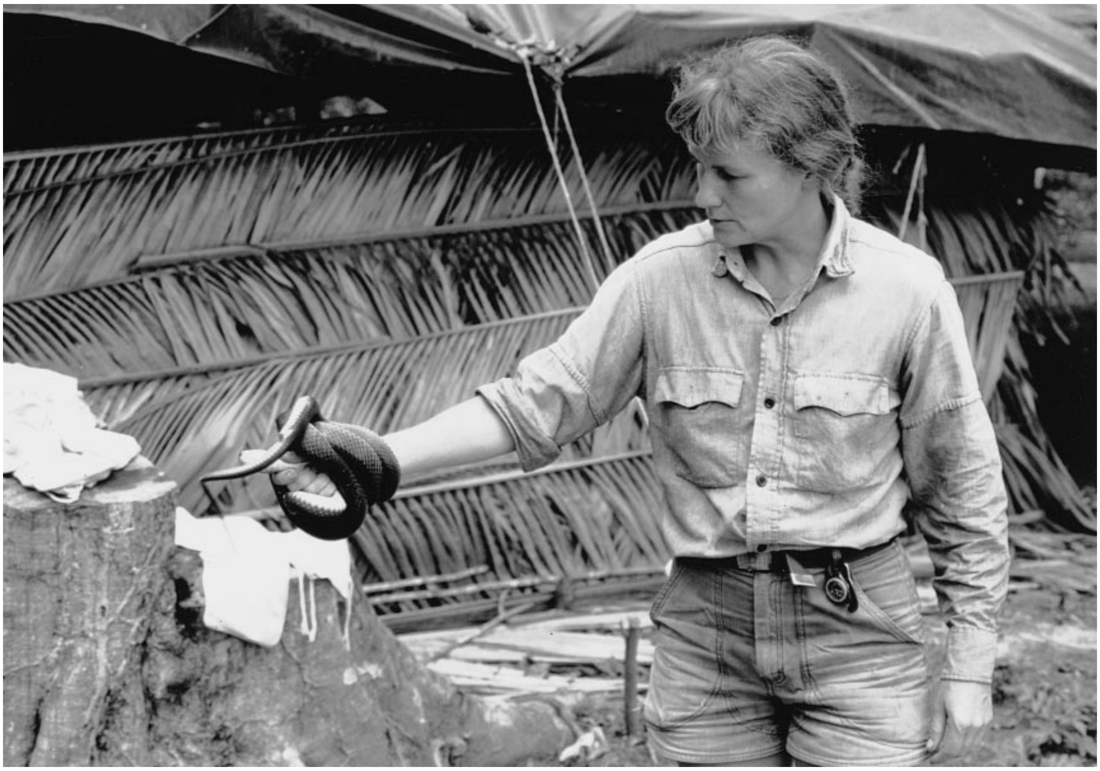

Fig. 111. Louise H. Emmons at the Rio Xingu camp. Photographed by M. D. Carleton in 1986.

> the same home country, they might be considered merely as color variations of one and the same species.

Wagner also gave these measurements: body, 6″ 4‴ [6¼ in.]; tail, 5″ 9‴ [5¾ in.]; ear, 0″ 7½‴ [⅔ in.]; hind foot, 1″ 5‴ [1½ in.]; our conversions to inches, indicated in brackets, are close approximations.[9]

The description seems to have been based on a single adult (coat color is certainly consistent with that typical of adults and not juveniles) collected by Johann Natterer from Ipanema, São Paulo, Brazil (there are several places with this name in southern Brazil, but the Ipanema Natterer used as his primary base is located at 23°26′S/47°36′W [Hershkovitz, 1987: 34; Paynter and Traylor, 1991: 294; Vanzolini, 1993: 27 and map on p. 28]; see locality 182 in gazetteer). Wagner did not identify the specimen he described by catalog number, and he did not designate a holotype.

Until now, Wagner's *russatus* has always been associated with *Holochilus*, as a possible synonym of *Hesperomys* (*Holochilus*) *physodes* (Burmeister, 1854: 167), a species of *Holochilus* (Trouessart, 1898: 521, 1904: 411; Fitzinger, 1867: 90; Gyldenstolpe, 1932: 63; Ellerman, 1941: 462), or listed in the synonymy of *Holochilus brasiliensis* (Hershkovitz, 1955: 661, 666; Cabrera, 1961: 505; Musser and Carleton, 1993: 704). Except for

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[9] The measurements in Wagner's account, those given by Lund (1840) and Burmeister (1854), and measurements referenced in other parts of the text and in the appendices, are the German zoll (two apostrophes) and linie (three apostrophes). In their exhaustive survey of measurement, Darton and Clark (1994: 524) indicated that a zoll is ‘‘an old Swiss measurement that was formerly just under 1 inch, 2.54 centimetres, and is generally translated as ‘inch' in modern dictionaries. When actually used today, however, the measure is ordinarily rounded up to 3 centimetres, 1.18 inch.'' Although Darton and Clark did not have an entry for linie, they (p. 250) describe a line as an infrequently used linear measure equivalent to one-twelfth of an inch. The German word linie translates to English as line. So the measurements are approximately in inches and twelfths of inches.

Burmeister's brief comparison of pelage color between *physodes* and *russatus* (1854; and see a translation of Burmeister's description in the account of *physodes* in Taxonomic Summary), no supporting evidence was ever provided for the association of *russatus* with *Holochilus*. We disagree with this historical allocation and document our identification of *russatus* in Taxonomic Summary, where we also designate a lectotype.

DISTRIBUTION, HABITAT, AND SYMPATRY

Specimens we identify as *Oryzomys russatus* come from three geographic regions (fig. 79). One extends through the forested foothills of the Andes from southern Bolivia at 18°11′S (locality 151 in gazetteer for *O. russatus*) to northern Argentina at 23°59′S (locality 170). Samples from this area have been identified as *O. legatus* in the literature. Another is in the cerrado region of south central Brazil along the Rio Paranaíba (locality 199) and near Anápolis (locality 200). Specimens from the Rio Paranaíba were described by Thomas (1901b) as *O. lamia*, and skin labels attached to the examples from Anápolis bear the same identification. The third segment is in southeastern Brazil east of the Rio Paraná throughout an area originally covered by tropical and subtropical evergreen rain forest. Our northernmost record is at 14°49′S in Estado da Bahia (locality 201); the southernmost is at 29°39′S in Estado do Rio Grande do Sul (locality 171). Samples from this broad area have been traditionally referred to as *O. intermedius*.

Our material certainly underestimates the range of *O. russatus*. In eastern Brazil, our southernmost record in Estado do Rio Grande do Sul likely reflects southern distributional limits of the species because it also coincides with approximate southern limits of subtropical forest (see vegetation map in Hueck and Seibert, 1981). However, the species probably occurs (or did at one time before modern deforestation) farther north than we have indicated because a strip of Atlantic rain forest historically extended up to ‘‘the level of Cape São Roque at 5° S, in the state of Rio Grande do Norte’’ (Por, 1992: 7, and map on p. 8; also, see the vegetative map in Hueck and Seibert, 1981). The vast region of cerrado and gallery forests between southern Bolivia and eastern Brazil is largely unsampled except for the biological reserves near Brasilia and the region around Anápolis and the Rio Paranaíba. We record *O. russatus* from the latter two places, but the species has apparently not yet been collected near Brasilia (Alho, 1982, Alho et al., 1986; Mares et al., 1989).

Apparently, the species also occurs on at least one island adjacent to the Brazilian coast. It has been documented, under the name *O. nitidus*, from São Sebastião Island (also known as Ilhabela; 23°50′S/45°20′W) off the northern coast of Estado do São Paulo (Olmos, 1996: 342), but was not encountered during a survey of islands off the coast of Estado Rio de Janiero (Fernandez et al., 1988).

Most collection records of *O. russatus* from the eastern segment of its distribution in Brazil are below 500 m, but the range is from sea level to 1000 m. For the western segment along foothills of the Andes, 2100 m in Departamento de Chuquisaca, Bolivia, and 500 m in Provincia de Salta, Argentina, bracket the range of elevations in which samples of *O. russatus* have been collected.

Habitat information was obtained from specimen labels, field notes, and published faunal reports and is summarized below by country.

Bolivia: Some of the specimens of *O. russatus* collected by members of the AMNH Bolivian Expedition (field notes in AMNH Mammalogy Archives) were captured in forest. The vegetation at **3 km WNW Caraparí** (locality 159) was described as ‘‘Humid forest on the slope of the brook, terrain very clayey and partially covered with leaf litter . . . temperate climate, terrain with some thorny shrubs,’’ and one specimen was caught ‘‘near spiny shrubs with leaf litter on gradient of 40° from the stream by the shoulder of a road’’ (August 1991). Near **Entre Ríos** (locality 160), three animals were collected in humid, dense forest (August 1991). And not far from **Cuyambuyo** (locality 163), a rat was caught in forest shading coffee trees (August 1991). Near **Estancia Las Cuevas** (locality 151), four specimens were collected during May 1991: AMNH 263182 and 265185 were captured on ‘‘bank of the river, on the other side from the camp that is young forest. The area has a small 'playa' . . . no canopy, shrub 10%, grass and other plants 90%''; AMNH 264184 was trapped in a place with ''no canopy, shrub 70%, grass and other plants 30% . . . sandy ground, vegetation green and abundant, little light reaches floor (10%). Humid. . . . Trapline 10 m from river . . . captured in well-shaded area''; and MSB 67321 was taken ''along edge of soccer field in heavy undergrowth, 15′ canopy, shady, leaf litter, forbes, vines. . . . Cover at shrub and ground level, 75%, canopy 80%.''

Argentina: Specimens from **Provincia de Salta** (localities 165 and 167 in gazetteer) were caught in ''lower subtropical Moist Forest'' and transitional forest (Mares et al., 1981b: 157) in a region where the dry season extends from about May through September and the summer rains, reaching 700 to 800 mm, begin in October and taper off in April (Mares et al., 1981b; Ojeda and Mares, 1989). *Oryzomys russatus* (discussed under ''*O. legatus*'') was found (Mares et al., 1981b: 174; on p. 158 they have a photograph of moist forest habitat and rocky banks along the Río Pescado):

> . . . only in mesic forests and transitional forests in the north-central portion of the province. They are not abundant in any area but are most common in littered forested areas supporting little undergrowth where they inhabit burrows in the forest floor. Some specimens were also taken in dense second growth vegetation along streams and roads, as well as from the rocky banks of the Río Pescado.

Ojeda and Mares (1989) noted that the examples of ''*O. legatus*'' were found in ''subtropical moist forest'' and ''lower montane forest.'' The former occurs between 350 and 500 m along the eastern slope of the Andes and is a ''deciduous transitional forest with trees from 20 to 30 meters tall, which abuts the eastern semiarid chaco and the montane forest communities.'' Lower montane forest in Salta Province ''is found between 500 to 1500 meters elevation. Trees vary from 20 to more than 30 meters in height. Shrubs, lianas, epiphytes, and grasses compose the other vegetational elements'' (p. 11). These two formations are basically the southern extensions of Bolivian transitional (''bosques mesofiticos de transición del Chaco marginal occidental,'' Hueck and Seibert, 1981) and Yungas forests (''pluviselva andina siempreverde, nivel inferior,'' Hueck and Seibert, 1981).

Brazil: Bergallo (1994) reported on ecology of the species (under *O. nitidus*) in the Atlantic Forest at the Juréia-Itatins Ecological Station (24°32′S/47°15′W) in Estado do São Paulo, southeastern Brazil. In a separate paper, Bergallo (1995) reported on life-history characteristics of the same sample, but under the name *intermedius*. The climate of the region is subtropical with high annual rainfall (3000–4000 mm), which falls mostly from December to March. Mean annual temperature ranges between 18.3 and 25.6°C. Hillsides, where the trapping grid was located, are covered by Atlantic rain forest with a canopy 20–30 m high; trees support a rich flora of epiphytes. Por and Imperatriz-Fonseca (l984) provided a more extensive description of the Reserve.

The country near **Anápolis** (locality 200) and along the Rio Paranaíba near Araguari (locality 199) consists of cerrado interspersed with tongues of eastern Brazilian tropical and subtropical forest along major rivers (Hueck and Seibert, 1981, designated it ''bosques subtropicales deciduos y mesofiticos del Brasil oriental y meridional, en parte con alta proporción de especies siempreverdes'' on their vegetation map). Brief notes describing habitat where specimens were collected at Anápolis during 1936 come from skin labels: ''edge of cornfield and woods'' (AMNH 134644, 134680); ''edge of corn fields and woods, brush'' (AMNH 134677); ''woods near cornfield'' (AMNH 134667); ''grass and brush near stream and heavy woods'' (AMNH 134665); and ''heavy grass, small stream, open woods'' (AMNH 134663).

In reporting the mammals obtained by A. Robert ''on the **Rio Jordão**'' (locality 199), which included the series described as *O. lamia*, Thomas (1901b: 527) commented that the collection ''was obtained in the tropical forest bordering the Paranahyba [= Rio Paranaíba], and therefore no doubt gives a sample of the fauna running northwards along that river into Goyaz.''

Among members of the former *O.* ''*capito*'' complex, the geographic range of *Oryzomys russatus* overlaps the distributions of *O. nitidus* in southern Bolivia, *O. megace-*

phalus in south-central Brazil, and *O. laticeps* in eastern Brazil, but we can record only a few places where it and other species discussed here were captured at the same locality. The area near Estancia Las Cuevas (locality 151) in southern Bolivia is one that we have already documented in the account of *O. nitidus*. Series of *O. megacephalus* (see sample 36 in appendix B where specimens are identified) and *O. russatus* were captured at Anápolis (locality 200) during the same period in 1936. Thomas (1901b) identified ''*Oryzomys laticeps*'' as occurring in the area from which A. Robert collected the type series of *O. lamia*. Both *O. russatus* and *O. laticeps* (see sample 47 in appendix B) have been taken at Ilhéus (locality 201) in Estado da Bahia, Brazil.

DESCRIPTION AND COMPARISONS

Oryzomys russatus is closely similar to *O. nitidus* and has a similar chromosomal composition (table 13), but differs by its larger body size, brighter pelage, larger and more robust cranium (figs. 98, 99, 112), and longer molar rows. See the account of *O. nitidus*, where we provide a full description of that species along with qualitative and morphometric comparisons between it and samples of *O. russatus*. The contrast in cranial and dental dimensions is documented by results from the various principal components and discriminant function analyses discussed in the account of *O. nitidus*, and can be visually appreciated in figures 98 and 99. Other than size (see table 37), the primary external difference between the two species is pelage coloration. Both species have tawny brown upperparts, but the dorsal coat of *O. russatus* is brighter due to the more intense saturation of ochraceous and buffy tones, especially along sides of the body.

Qualitative contrasts between *Oryzomys russatus* and other members of the former *O.* ''*capito*'' complex parallel those seen between *O. nitidus* and the species of the *O. megacephalus* and *O. yunganus* groups, contrasts we discussed in the account of *O. nitidus*.

GEOGRAPHIC VARIATION

In the previous account of *Oryzomys nitidus*, we described the pattern of intersample variation in pelage coloration and cranial and dental dimensions between samples of *O. nitidus* and those formerly known as *O. legatus*, *O. lamia*, and *O. intermedius* (= *russatus*). These taxa identify the three distinct geographical components within *O. russatus* as distinguishable primarily by differences in cranial dimensions: the sample of *lamia* from south-central Brazil (Anápolis and Araguari) averages larger than do examples of *russatus* from southeastern Brazil, and the series of *legatus* from southern Bolivia and northern Argentina lies between those extremes (see the canonical variate scatterplots in figs. 96 and 97). This morphometric pattern is mirrored by clustering analysis with Mahalanobis' distances among centroids, the results of which retain the integrity of each set of geographic samples; however, clustering based on mean cranial and dental sizes (Euclidean Distance) blurs the separation of *legatus* and *russatus* while still highlighting the distinctness of *lamia* (fig. 100).

We also pointed out in the account of *O. nitidus* that visual inspection of specimens combined with morphometric analyses suggested closer resemblance between samples of *legatus* and *lamia* than between those entities and series of *russatus*. Compared with that form, available specimens from southern and northern Bolivia and south-central Brazil share a more robust cranium and a brighter dorsal pelage that results from ochraceous bands being more intensely saturated along the sides of the body with highlights extending over more of the body.

For the reasons previously discussed in the *O. nitidus* account, we favor the hypothesis that these three sets of samples represent geographic segments of one species. Distribution of our samples suggests the three units are currently isolated from one another, but this pattern may simply reflect inadequate sampling from intermediate regions. Today, extensive Chacoan habitats lie between the western population of *O. russatus* in southern Bolivia and northern Argentina and the one in southeastern Brazil (see the vegetation map in Hueck and Seibert, 1981). Still, some broad tongues of forest habitat in the Anápolis region and along the upper reaches of the Rio Paranaíba in south-central Brazil merge with tropical and subtropical forma-

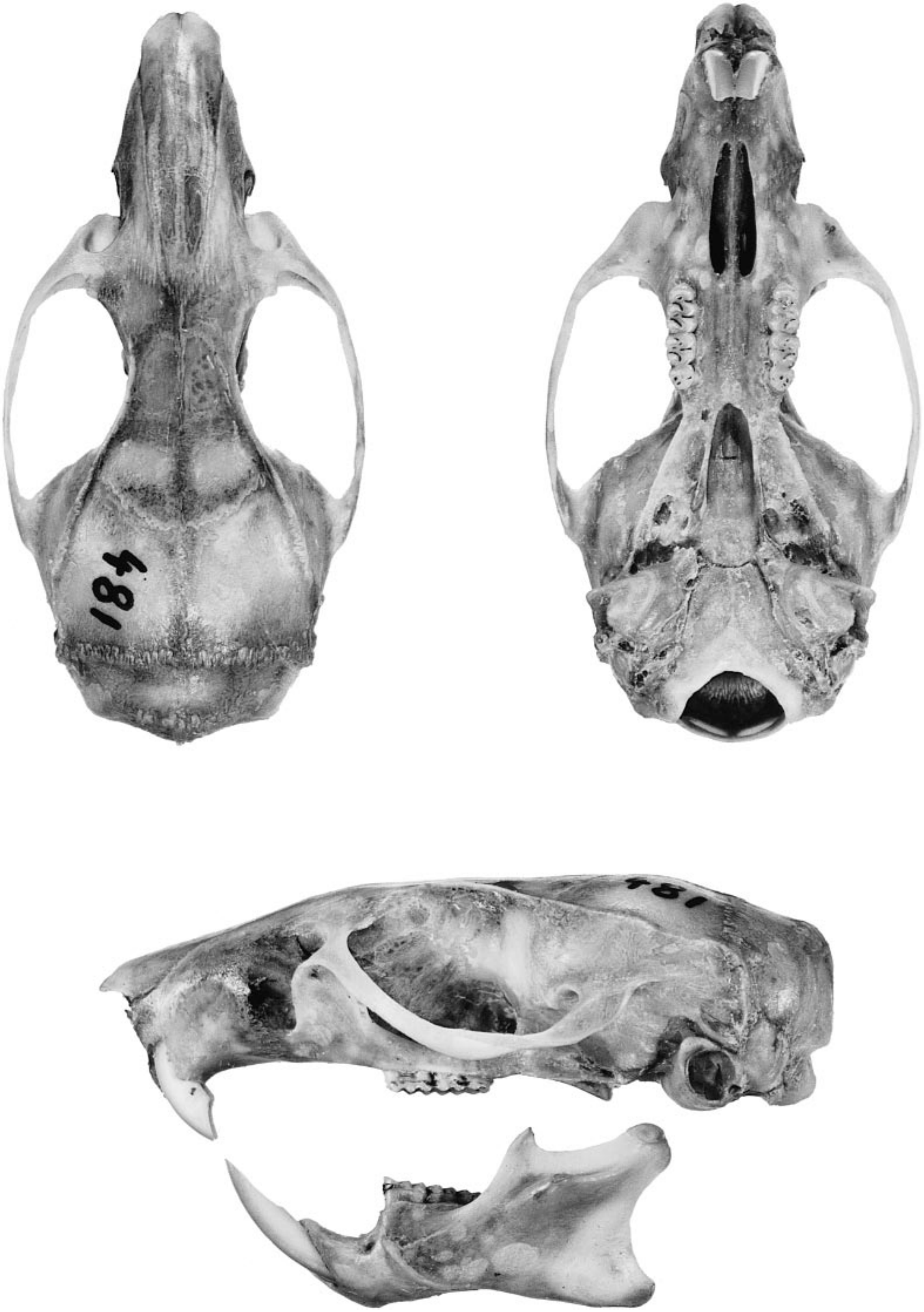

Fig. 112. Cranium and dentary of *Oryzomys russatus* (NMW B481, a syntype), an adult male from Ipanema, Estado de Minas Gerais, Brazil. ×3.

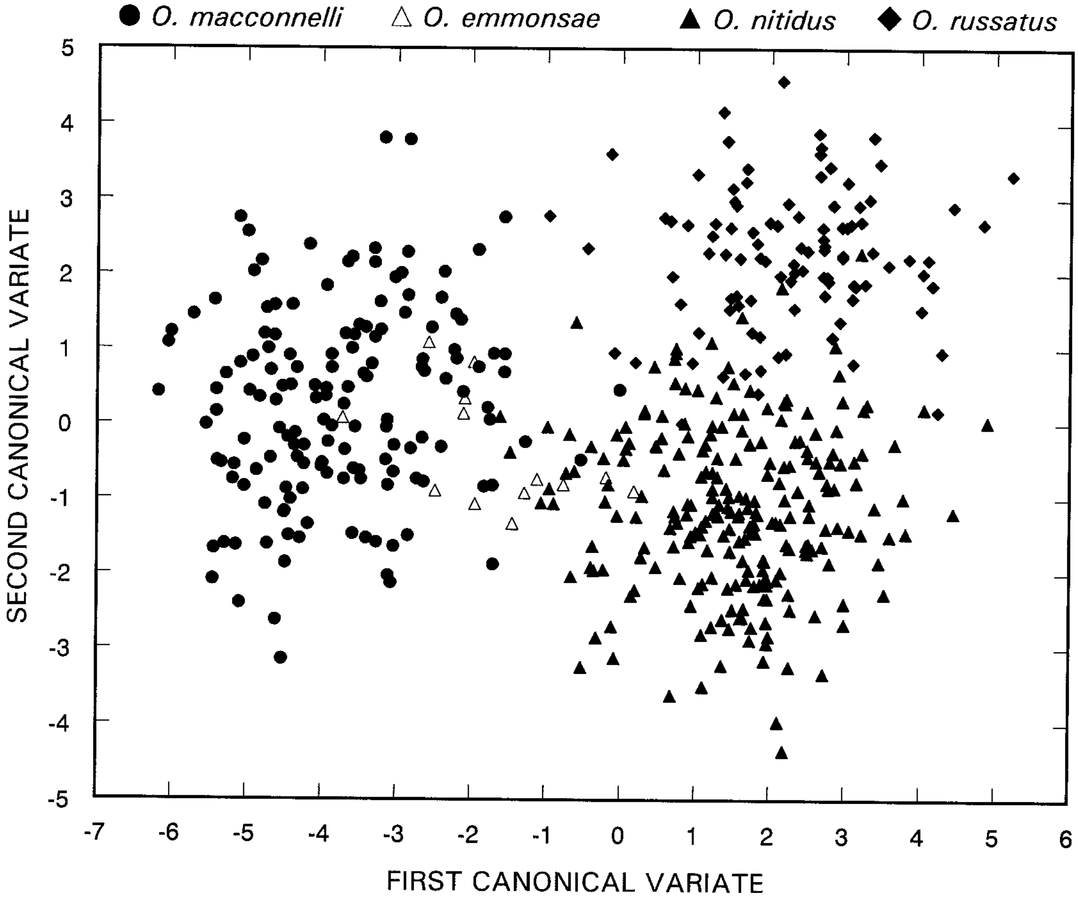

Fig. 113. Individual specimen scores based on log-transformed values of 13 cranial and two dental variables (see table 46) and projected onto the first and second canonical variates derived from discriminant function analysis of 24 population samples (table 39) representing *Oryzomys macconnelli* (samples 1–8, *N* = 151), *O. nitidus* (samples 9–17, *N* = 23), *O. emmonsae* (sample 18, *N* = 14), and *O. russatus* (samples 19–24, *N* = 103). Also see figure 114.

tions of eastern Brazil, where most samples of *O. russatus* were obtained. If not deforested, a transect through this region—from Anápolis to Belo Horizonte, for example—might reveal whether the *lamia* morphology intergrades with the eastern *russatus* form. Determining whether western populations of *O. russatus* (the "*legatus*" morphology) are geographically (or genetically) isolated from the others would require surveys in the mosaic of subtropical and deciduous forests, cerrado, and Pantanal between southern and eastern Bolivia and the Anápolis region, an extensive area that has received little intensive survey efforts for small mammals.

The zoogeographic affinity between populations found along the eastern Andean foothills and those in eastern Brazil, as indicated by the disjunct distribution of *Oryzomys russatus* (that is, disjunct as reflected by our recorded localities, which may reliably estimate the actual range or represent sampling artifact), extends to another oryzomyine. The species currently known as *Oryzomys ratticeps* ranges throughout eastern Brazil from the states of Minas Gerais (Ávila-Pires, 1959c) and Espírito Santo (specimens in LACM) south to Rio Grande Do Sul (Hensel, 1872; Ávila-Pires, 1994; Thomas, 1924) and, like *O. russatus,* also occurs in northwestern Argentina in Provincia de Jujuy (specimens stored at OMNH and

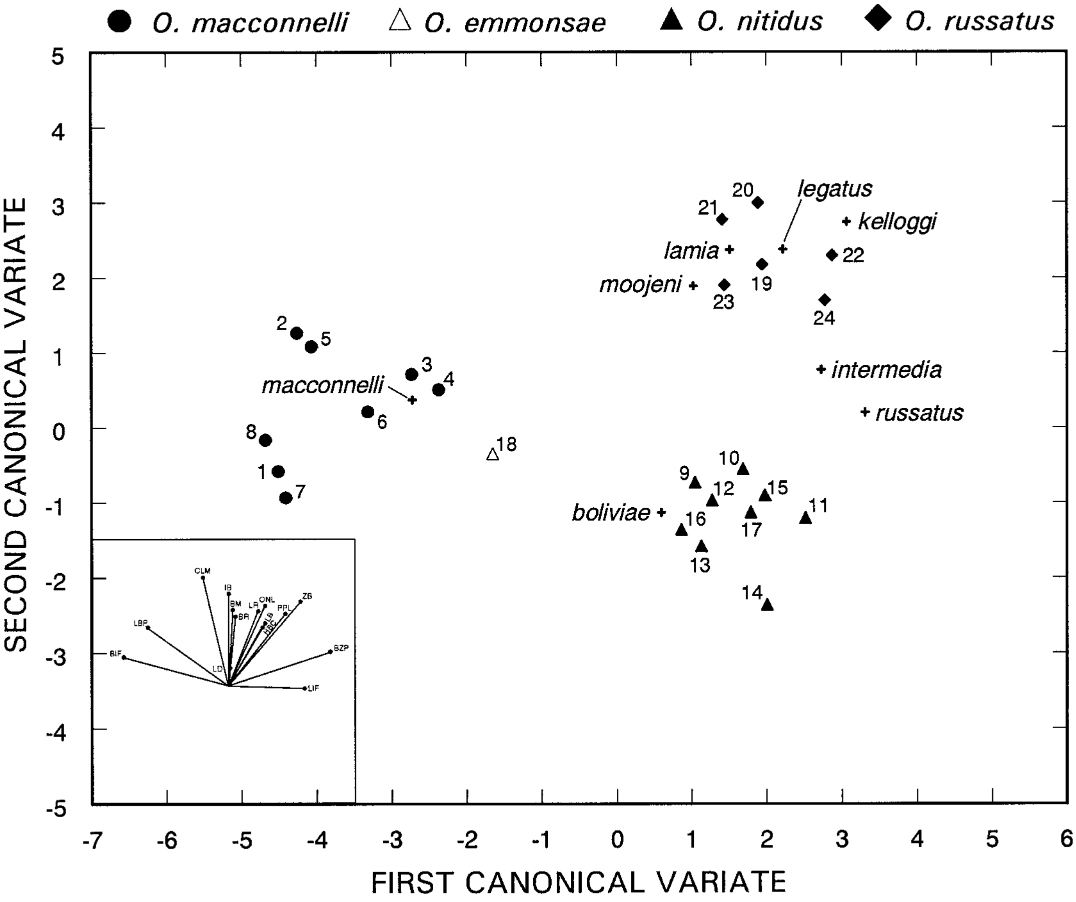

Fig. 114. Plot of group centroids on first two canonical variates derived from discriminant function analysis of 24 population samples representing *Oryzomys macconnelli* (samples 1–8), *O. nitidus* (samples 9—17), *O. emmonsae* (sample 18), and *O. russatus* (samples 19–24). Also see figure 113. Scores of pertinent holotypes (*macconnelli*, *boliviae*, *emmonsae*, *russatus*, *intermedia*, *lamia*, *legatus*) and paratypes (*kelloggi* and *moojeni*) derived from posterior probabilities of group membership are also pictured. **Inset:** Vectors of 15 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (also see table 46).

sent by M. Mares to G. Musser for identification); however, in contrast to that species, *O. ratticeps* has also been recorded from northeastern Argentina (Massoia et al., 1987) and eastern Paraguay (Myers, 1982).

SUMMARY

Our study of 921 specimens representing the *nitidus* complex leads us to accept the hypothesis that this material represents four biological species. *Oryzomys macconnelli* inhabits pristine tropical rainforest habitats in Amazonia. Its geographic range overlaps that of *O. nitidus*, which ranges through western Amazonia along the base of the Andes from Perú to Bolivia and eastward through southern Brazil to eastern Paraguay and northeastern Argentina. *Oryzomys russatus* occurs in rain forests of south-central and eastern Brazil as well as along the Andean foothills in southern Bolivia and northern Argentina. Its range is largely allopatric to that of *O. nitidus* except in southern Bolivia, where the two are sympatric. *Oryzomys emmonsae* is known only from lowland tropical rain forest in Amazonia south of the Rio Amazonas along the lower reaches of the Rio Xingu and Rio Tocantins.

The four species closely resemble one another in their pelage coloration and body proportions. The dorsal coat of *Oryzomys macconnelli* has a richer sheen, is longer, and feels more luxuriant to the touch than do upperparts of the other three; the tail is longer relative to length of head and body in *O. emmonsae;* and upperparts of *O. russatus* are brighter due to the increased extent of ochraceous tones in the dorsal pelage, most vividly expressed by individuals in populations from south-central Brazil and along the Andes in southern Bolivia and northern Argentina.

All four species share the same general cranial conformation and very similar molar occlusal patterns. Differences among the species are reflected primarily by variation in dimensions and proportions as summarized by the various morphometric analyses (figs. 113, 114). Separation of individual scores and group centroids along major axes reveals that relative to *Oryzomys macconnelli, O. nitidus* and *O. russatus* possess longer crania, greater zygomatic breadths, longer rostra, wider occipital regions and deeper braincases, broader zygomatic plates, and longer postpalatal regions; however, they have narrower interorbits and rostra, longer but narrower incisive foramina, correspondingly shorter bony palates, and modestly shorter molar rows (table 46). Other than size, the proportional contrasts of some cranial variables strongly distinguish *O. nitidus* and *O. russatus* from *O. macconnelli*; the latter has a relatively broader rostrum and interorbit, narrower zygomatic plate, shorter and wider incisive foramina, and longer bony palate. Compared with specimens of *O. nitidus*, examples of *O. russatus* have larger crania, longer molar rows, and relatively shorter incisive foramina.

Our initial identification problems with the Pará Sample, which we have named *O. emmonsae,* is partly explained by its intermediate morphology, as reflected by the intermixing of individual specimen scores within the constellations for *O. macconnelli* and *O. nitidus* along the first canonical variate (fig. 113). The group centroid for the sample of *O. emmonsae* falls between those clusters representing *O. nitidus* and *O. macconnelli,* but is closer to the latter (fig. 114), indicating its resemblance to *O. macconnelli* in proportions of the interorbit, zygomatic plate, incisive foramina, and bony palate (as described and illustrated in the comparative sections of the *O. nitidus* account). A qualitative feature also separates *O. emmonsae* and *O. macconnelli* from *O. nitidus* as well as from *O. russatus*; alisphenoid struts are absent from most specimens of the former pair, but present in about half the examples surveyed in the latter two. On the other hand, *O. emmonsae* and *O. nitidus* share a similar karyotype unlike that of *O. macconnelli.*

Scores of holotypes and paratypes derived from posterior probabilities of group membership suggest the phenetic affinities of these specimens. The taxa *lamia, legatus,* and *kelloggi,* originally described as distinct

TABLE 46

Results of Discriminant Function Analysis of 24 Population Samples Representing *Oryzomys macconnelli* (Samples 1–8), *Oryzomys nitidus* (Samples 9–17), *Oryzomys emmonsae* (Sample 18), and *Oryzomys russatus* (Samples 19–24)

(Localities constituting each sample as well as sample size are listed in table 39, mean values for measurements of variables in each sample are indicated in appendix E, and specimens measured are identified in appendix F. See figs. 113 and 114.)

Variable	Canonical variates First	Canonical variates Second	*F* (Sample)[a]
ONL	0.28	0.59	14.1
ZB	0.53	0.62	24.8
IB	0.00	0.68	17.9
LR	0.22	0.55	11.1
BR	0.05	0.51	7.9
LB	0.27	0.46	10.6
HBC	0.25	0.43	7.9
BZP	0.75	0.25	33.5
LD	0.01	0.13	5.8
LBP	−0.60	0.43	30.3
PPL	0.42	0.53	15.0
LIF	0.55	−0.02	16.5
BIF	−0.78	0.21	40.1
CLM1-3	−0.18	0.80	22.8
BM1	0.03	0.56	10.0
Canonical correlation	0.94	0.82	
Eigenvalue	7.12	2.03	
% Variance	56.8	16.2	

[a] All *F* values are significant at $P \leq 0.001$.

species (Thomas, 1924, 1925; Ávila-Pires, 1959a) and so recognized in a current checklist (Musser and Carleton, 1993), fall within the population samples of *Oryzomys russatus* (fig. 114). Scores for *intermedia*, described as a variety of ''*Hesperomys laticeps*'' (Leche, 1886), and *moojeni*, proposed for a subspecies of *Oryzomys ratticeps* (Ávila-Pires, 1959b), are also part of the *O. russatus* cloud.

Integrity of sample groupings for *O. macconnelli* and *O. nitidus* is maintained in both cluster diagrams (fig. 115), reflecting the lack of appreciable geographic variation among the samples of each species. *Oryzomys emmonsae* associates distantly with *O. macconnelli* in the Mahalanobis' arrangement, but nestles within the samples of *O. macconnelli* in the Euclidean pattern, indicating again that *O. emmonsae* is morphometrically closer to *O. macconnelli* than to *O. nitidus*, despite its apparent chromosomal similarity with the latter. The samples of *O. russatus* from eastern Brazil (*russatus* morph) and the Andean foothills in southern Bolivia and northern Argentina (*legatus* morph) cluster closely in the Euclidean diagram, but not in the pattern based on Mahalanobis' distances; the sample from south-central Brazil (*lamia* morph) is distantly associated with other samples of *O. russatus* in both clustering arrangements. This conflict either signifies the appreciable geographic variation among measured samples from the three regions or indicates that examples of the three morphs—*russatus*, *legatus* and *lamia*—represent three biological species.

Another set of summary data supports our hypothesis of species definitions, but provides a slightly different interpretation of relationships among them. James L. Patton (letter in AMNH Mammalogy Archives) provided us with results of maximum parsimony analysis of 801 base pairs of mitochondrial cytochrome-b sequence for five specimens of *Oryzomys macconnelli*, two *O. russatus*, two *O. emmonsae*, and one example of *O. nitidus*, rooted with a sequence from *O. megacephalus* (fig. 116; the tree is extracted from results from a larger study analyzing additional species and specimens from a broader geographic region that will be reported by J. L. Patton and his colleagues). The sequence data indicated a link between *O. macconnelli* and *O. russatus*, although not a strong one (the bootstrap value is less than 50), an association counter to our interpretation of pelage features, morphometric traits, and chromosomal composition, which points to a sister-group relationship between *O. russatus* and *O. nitidus*. On the other hand, the position of *O. emmonsae* in the tree, between *O. nitidus* and *O. macconnelli*–*O. russatus*, partly concurs with the estimate of its relationship derived from discriminant function analysis. Patton noted in his letter that the groupings are ''about equidistant from one another, and the distances are quite large (about 10% on average),'' which he claims supports separate species status for each. On the other hand, R. S. Voss pointed out to us that because the node grouping *O. macconnelli* with *O. russatus* has a bootstrap value of less than 50, it does not indicate strong support for that link; the relationships of *O. macconnelli*, *O. russatus*, and *O. emmonsae* are not well resolved by the sequence data.

We caution readers that our definitions of the four species are presented as hypotheses to be tested by analyses of larger samples from some of the poorly surveyed geographic regions and of new material from the broad expanses of unsampled areas. We are comfortable with the morphological limits indicated for *O. nitidus*, *O. macconnelli*, and *O. emmonsae*, but are distinctly unsatisfied with our definition of *O. russatus*. Arranging samples obtained along the Andean foothills in southern Bolivia and northern Argentina with those collected in south-central Brazil along with the samples from eastern Brazil into one biological species may or may not reflect reality—only analyses of new specimens from currently unsampled geographic areas can settle this uncertainty.

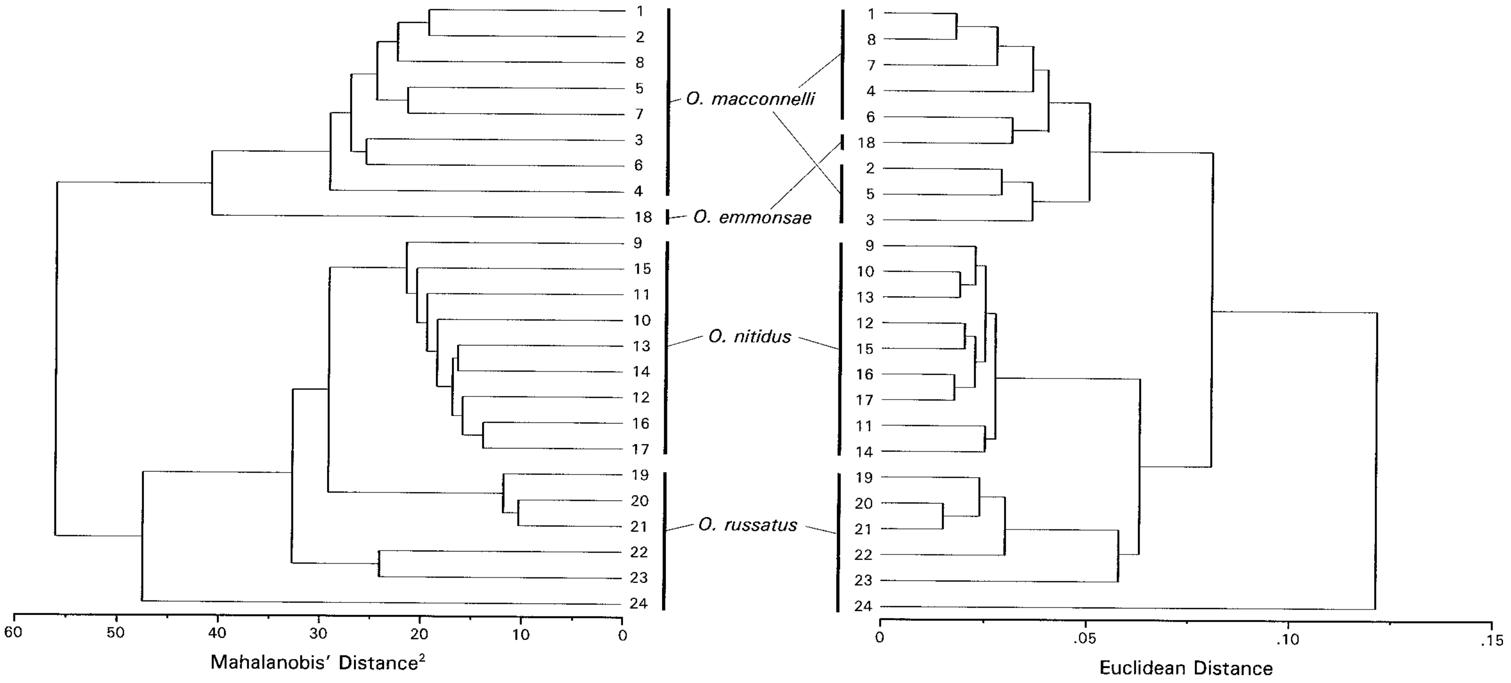

Fig. 115. UPGMA clustering of 24 population samples of *Oryzomys macconnelli* (samples 1–8), *O. nitidus* (samples 9–17), *O. emmonsae* (sample 18), and *O. russatus* (samples 19–24) generated from Mahalanobis' distances (D^2) among group centroids (see fig. 114). Euclidean distances between samples are based on log-transformed means of 15 cranial and dental variables. Localities constituting each sample and size of sample are indicated in table 39, mean values of measurements for variables are listed in appendix E, and specimens measured are identified in appendix F.

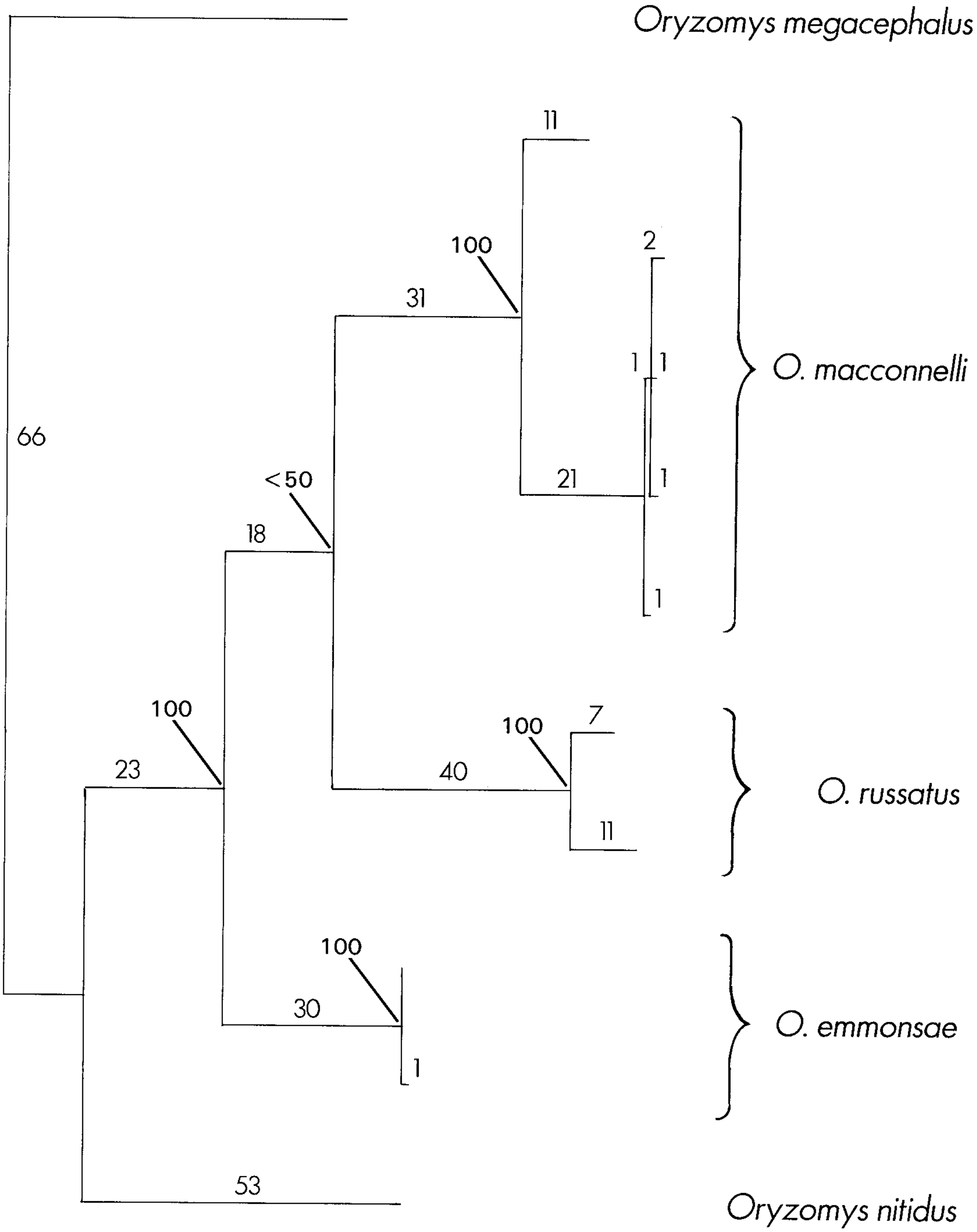

Fig. 116. Maximum parsimony analysis of 801 base pairs of mitochondrial cytochrome-b sequence (see Patton et al., 1996) for ten specimens in the *Oryzomys nitidus* group, rooted with a sequence from *O. megacephalus*. Tree length = 318 steps, CI = 0.790, RI = 0.779, and RC = 0.601. Numbers on the branches refer to number of character changes; bold numbers at the nodes are bootstrap values (the number of times in 100 bootstrap resamplings that a particular node was identified, providing an estimate of the strength of a given node). Individual haplotypes (specimens) are listed below following order of terminal twigs from top of the tree down:

O. megacephalus

TAXONOMIC SUMMARY

This penultimate section of our report is devoted to summarizing the scientific names we associate with each species in the former *Oryzomys* ‘‘*capito*’’ complex, providing emended diagnoses and abbreviated geographic distributions, and defending our allocations of scientific names. We include a discussion of the scientific names that should be associated with species in the *Oryzomys subflavus* group because confirming their identities was related to uncovering the correct oldest names applying to some of the species in the *Oryzomys nitidus* group.

SCIENTIFIC NAMES ASSOCIATED WITH SPECIES IN THE FORMER *ORYZOMYS* ‘‘*CAPITO*’’ COMPLEX

ORYZOMYS MEGACEPHALUS

Mus megacephalus Fischer (1814: 71), based on Azara’s (1801: 82) ‘‘Rat second, ou Rat à grosse tête.’’ NEOTYPE: UMMZ 133811 (stuffed skin, fig. 117; skull, fig. 118; intact dentition, fig. 119; carcass in fluid, chromosomal spreads, fig. 11; measurements listed in table 47), a young adult male collected July 18, 1979 by P. Myers. TYPE LOCALITY: Paraguay east of the Río Paraguay, Departamento de Canendiyu, 13.3 km (by road) N Curuguaty (24°31′S/55°42′W), 255 m (Paynter, 1989: 12; also see map in Myers and Carleton, 1981).

Mus capito Olfers (1818: 209). A second name applied to Azara’s ‘‘Rat second, ou Rat à grosse tête.’’

Mus cephalotes Desmarest (1819: 63). A third name based solely on Azara’s description of ‘‘Rat second, ou Rat à grosse tête.’’

Oryzomys velutinus Allen and Chapman (1893: 214). TYPE LOCALITY: Trinidad, Princestown (10°16′N/61°23′W). HOLOTYPE: AMNH 5949/4679 (skin and skull, figs. 120, 121; measurements listed in table 47), an adult male collected April 16, 1893 by F. M. Chapman.

Oryzomys goeldi Thomas (1897: 494). TYPE LOCALITY: Brazil, Estado de Pará, Itaituba, Rio Tapajós (04°17′S/55°59′W). HOLOTYPE: BMNH 97.4.1.1 (skin and skull, figs. 120, 121; measurements listed in table 47), a young adult female given to the British Museum by E. A. Goeldi.

Oryzomys modestus Allen (1899: 212). TYPE LOCALITY: Venezuela, Estado de Sucre, Campo Alegre (10°10′N/63°45′W, Paynter, 1982: 26) 3000 ft. HOLOTYPE: AMNH 14734 (skin and skull, figs. 120, 121; measurements listed in table 47), a young adult female collected November 20, 1898 by F. W. Urich.

Oryzomys perenensis Allen (1901: 406). TYPE LOCALITY: Perú, Departamento de Junín, Perené (10°06′S/75°13′W), 800 m. HOLOTYPE: BMNH 0.7.7.25 (skin and skull, figs. 117, 118; measurements listed in table 47), an adult male collected April 11, 1900 by P. O. Simons.

EMENDED DIAGNOSIS: An oryzomyine of moderate body size with tail shorter than length of head and body; brownish tawny upperparts characterized by flat or burnished tones, sides of head and body only slightly paler, grayish white underparts; tail monocolored or mottled on ventral surface; dorsal

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1. Perú: MVZ 166676.

O. macconnelli (all are from Estado do Amazonas, Brazil)
2. MNFS 747: Barro Vermelho, left bank Rio Juruá.
3. JUR 355: Colocaço Vira-Volta, left bank Rio Juruá on Igarapé Arabidi, affluent of Paraná Breu.
4. JUR 386: Lago Vai-Quem-Quer, right bank Rio Juruá.
5. MNFS 84: alto Rio Urucu.
6. MNFS 156: alto Rio Urucu.

O. russatus (both are from Estado do São Paulo, Brazil)
7. ML 48: Fazenda da Toca, Ilhabela, Ilha São Sebastião.
8. ML 49: Fazenda da Toca, Ilhabela, Ilha São Sebastião.

O. emmonsae (both are from Estado de Pará, Brazil)
9. USNM 549552: right bank Rio Xingu, 52 km SSW Altamira.
10. MZUSP 27150 (holotype): right bank Rio Xingu, 52 km SSW Rio Altamira.

O. nitidus
11. MNFS 1419: Igarapé Porongaba, right bank Rio Juruá, Estado do Acre, Brazil.

surfaces of front and hind feet white, claws covered by dense silvery ungual tufts, plantar surface with six tubercles; superciliary, genal, and mystacial vibrissae long enough to reach posterior margin of ear but not to extend beyond; cranium with moderately short rostrum, wide interorbit with smooth dorsolateral margins except in old animals (slightly ridged), alisphenoid struts absent, zygomatic plate narrow relative to cranial length (compared with *O. yunganus*); incisive foramina short and wide (together they form a teardrop outline), bony palate long; modified cephalic arterial pattern indicated by lack of both sphenofrontal foramen and squamoso-alisphenoid groove, but presence of large stapedial foramen and prominent groove for infraorbital branch of stapedial artery on ventral, posterolateral portion of pterygoid plate; second upper molar with long paraflexus and labial fossette only (no medial fossette); second lower molar nearly bisected by elongate hypoflexid, entoflexid shallow, no fossettid; chromosomes $2n = 52$ and $\mathrm{FN} = 62$ in western portion of geographic range and correlates with large body size, $2n = 54$ and $\mathrm{FN} = 62$ or 58–59 (Surinam) in eastern part of range and associated with smaller body size.

DISTRIBUTION: Tropical and subtropical rain forests of Amazonia and eastern Paraguay.

DESIGNATION OF NEOTYPE FOR *MEGACEPHALUS*: Some specimens described by Azara are preserved in museum collections. There is, for example, a holotype for *Caluromys lanatus* in the Museo de Ciencias Naturales, Madrid, which was collected by Azara (Hershkovitz, 1987: 60), and in his account of *Vampyrops lineatus*, Cabrera (1958: 81) also discussed some of Azara's specimens. We have never seen reference to any of Azara's rodent specimens and assume they do not exist. Therefore, a neotype must be selected for *Mus megacephalus* Fischer (1814). The circumstance meets the requirement of article 75a of the *International Code of Zoological Nomenclature* (1985 edition): ''A neotype is to be designated only in connection with revisory work, but only in exceptional circumstances when a neotype is necessary in the interests of stability of nomenclature . . .'', and provision i of article 75b explains that '' 'revisory work' refers to a critical study of the nominal species-group taxon in question, regardless of the scope of the work in which it is published.''

Myers (1982) indicated that ''*Oryzomys capito*'' occurs in Paraguay only east of the Río Paraguay, a region originally covered with subtropical and tropical forest, vegetative formations that are a southwestern extension of the Atlantic Forest region of Brazil (see the vegetation map in Hueck and Seibert, 1981). The specimens Azara (1801: 82) described certainly came from eastern Paraguay, apparently from the vicinity of San Ignacio Guazú, which is in the southern part of the country in Departamento de Las Misiones, about 190 km SSE of Asunción. Paraguayan specimens used in the analyses were collected by P. Myers, who did not obtain material from southern Paraguay but did collect specimens from localities farther north (sample 43; table 1). Of the samples he sent us to study, the largest series is from the Departamento de Canendiyu, 13.3 km N of Curuguaty (24°31′S/55°42′W) in east-central Paraguay east of the Río Paraguay. Among them is a well-preserved young adult male (UMMZ 133811) captured by P. Myers (field number 4186) on July 18, 1979 that we designate as neotype for *Mus megacephalus* Fischer (1814: 71), which, to our knowledge, is the oldest name available for Azara's (1801: 82) ''Rat second, ou Rat à grosse tête.''

The neotype consists of a conventional stuffed museum skin (fig. 117), cranium and mandible (fig. 118), intact dentition (fig. 119), carcass preserved in fluid (originally fixed in formalin solution and subsequently transferred to a mixture of ethanol and water; the carcass is undissected, the genitalia intact), and chromosomal preparations (fig. 11). External, cranial, and dental measurements (including weight) are listed in table 47.

The neotype is of moderate body size with a tail shorter than the combined length of head and body (table 47). Upperparts are tawny brown from nose to base of tail, darker and richer along the middorsal region, and somewhat brighter along sides of the body. Aside from a dark brown eyelid, the facial region lacks distinctive patterning. The dorsal pelage is soft and moderately long (up to

Fig. 117. Dorsal and ventral views of stuffed study skin representing the neotype (UMMZ 133811) of *Mus megacephalus* Fischer (1814). Measurements are listed in table 47.

8 mm over lower part of back and rump). Underparts are grayish white (overhairs gray for two-thirds their lengths and tipped with white) and sharply demarcated from the dorsum. The coloration extends onto the head near bases of the facial vibrissae. Ears are dark brown and densely covered with fine brown and silvery hairs. Mystacial, genal, and superciliary vibrissae are moderately long, extending to the posterior margins of the ear (when appressed against the body). The tail is tan on all surfaces and finely haired. Dorsal surfaces of front and hind feet are white, an effect produced by their dense covering of frosty hairs. Dense ungual tufts nearly conceal the claws and extend well beyond their tips. A large thenar, small hypothenar, and four interdigital pads adorn the brown plantar surface. The proportion of the hind digits in relation to each other and to the metatarsus is closely similar to that illustrated for the specimen of *O. megacephalus* in figure 17.

The cranium is elongate and somewhat stocky. From a dorsal perspective, the rostrum is wide but not long, the interorbit is wide and outlined by smooth dorsolateral margins, the zygomatic notches are deep, and the braincase squarish. The large interparietal roofs a moderately deep (anterior–posterior) occipital region. In ventral view, the short and wide incisive foramina are distinctive, as is the long bony palate. Short slits pierce the roof of the mesopterygoid fossa. Anterior portions of the pterygoid fossae are complete except for minute perforations. The auditory bullae are small and globular. Each zygomatic plate, as seen in lateral view, is broad and correlates with the deep zygomatic notches. The alisphenoid regions are without struts, and the postglenoid foramen is spacious and separated from a wide subsquamosal fenestra by an elongate hamular process of the squamosal. The tegmen tympani of the periotic does not extend anteriorly to overlap the squamosal, a configuration seen in figure 118 and diagramed by Voss (1993: 19). A modified cephalic arterial circulation is present, as indicated by the absence of sphenofrontal foramina and squamosoalisphenoid grooves and by the presence of large stapedial foramina and a deep furrow in the posterolateral portion on the ventral surface of each pterygoid plate, as illustrated for *O. yunganus* and *O. megacephalus* (fig. 27). This configuration, as Carleton and Musser (1989: 35) described it, indicates ‘‘that the supraorbital branch of the stapedial artery is absent and that the orbital supply arises instead from the distal part of the infraorbital branch. . . . the infraorbital continues as an extension of the stapedial through the alisphenoid canal and emerges onto the orbital through the anterior alar fissure. The infraorbital's passage ventral to the posterior edge of the pterygoid plate is marked by an external groove.’’ The combination of bony traits and foramina indicates a cephalic pattern closely similar to that described and illustrated for species of *Oligoryzomys* (Carleton and Musser, 1989).

Each dentary is robust. The coronoid process is slender, and the posterior margin between condyloid and angular processes is concave.

Enamel layers of incisors are pale yellowish orange. The uppers are opisthodont in configuration relative to the axis of the rostrum. Molars are brachydont and cuspidate. Distinctive traits are exemplified by occlusal patterns of second upper and lower molars (fig. 119). A deep paraflexus is present, along with only one labial fossette, which represents the uncoalesced portion of the mesoflexus (the fold between paracone and mesoloph), which is indicated on the labial surface by only a shallow indentation. In each second lower molar, the hypoflexid is long, the entoflexid indiscernible, and a fossettid lacking.

Chromosomal characteristics of the neotype are illustrated in figure 11. The $2n$ is 54 and the FN is 62; autosomes consist of five pairs of medium-sized to small metacentrics and submetacentrics and 21 pairs of telocentrics; the sex chromosomes consist of a large telocentric X and a small telocentric Y (see table 13).

In addition to the neotype, we examined other specimens collected at the same locality. Six (UMMZ 126010, 126011, 133801, 133802, 133804, and 133807) are in full adult pelage and closely resemble the holotype in coloration and pelage characteristics. Females have four pairs of mammae (one pectoral, one postaxillary, one abdominal,

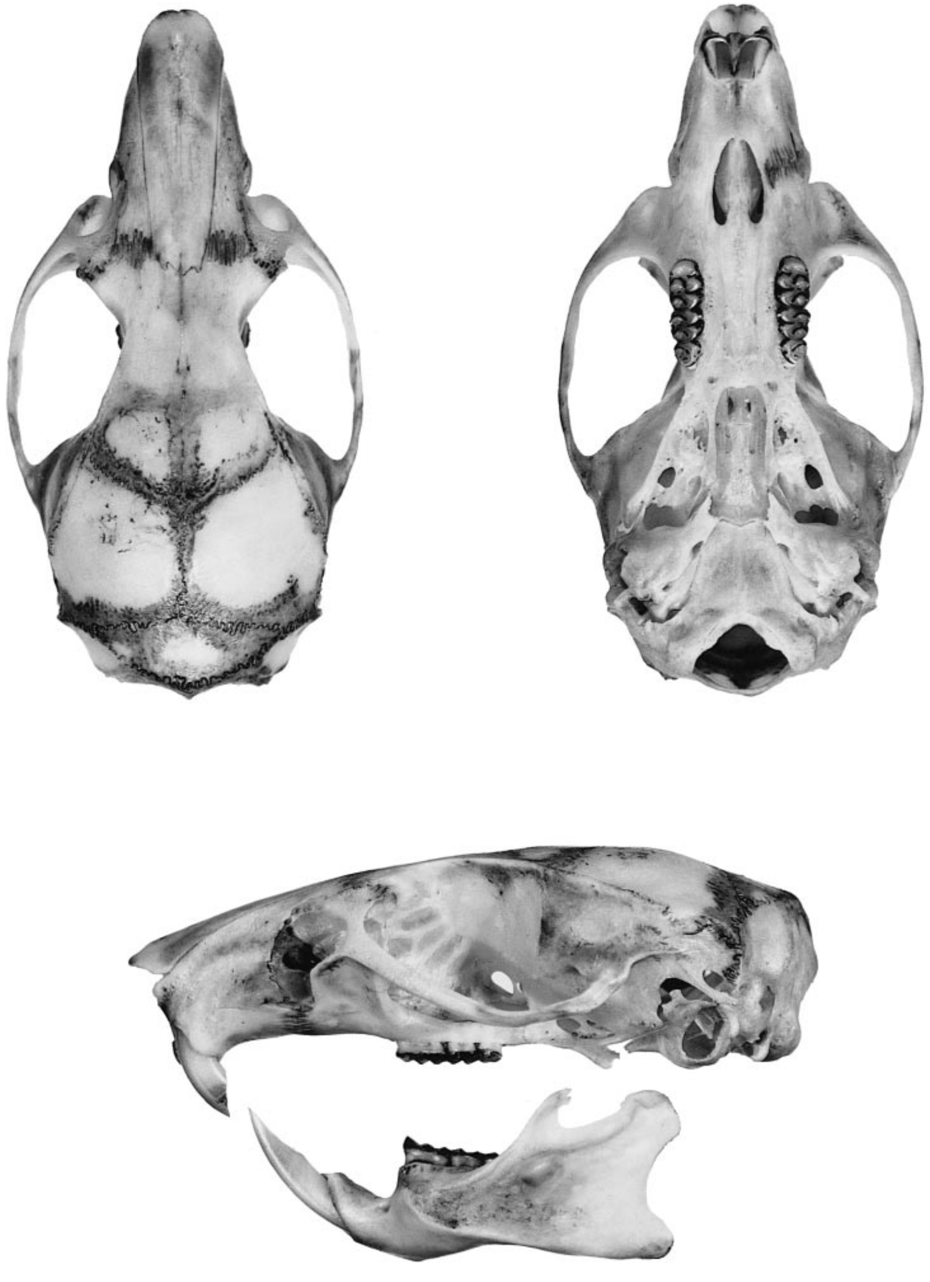

Fig. 118. Cranium and dentary of the neotype (UMMZ 133811) of *Mus megacephalus* Fischer (1814), a young adult male from near Curuguaty, eastern Paraguay (a member of sample 43 in table 1). Skin and molar rows are illustrated in figures 117 and 119, respectively. Measurements are listed in table 47. See text for additional information about the specimen. ×3.

and one inguinal). Two examples (UMMZ 133809 and 133812) are clothed in mostly adult pelage, patches of which were partly emerged through the skin. These coats are slightly darker and duller than those seen on full adults. Five specimens are in various stages of molt from juvenile to adult pelage. Of these, UMMZ 133806 is in full juvenile

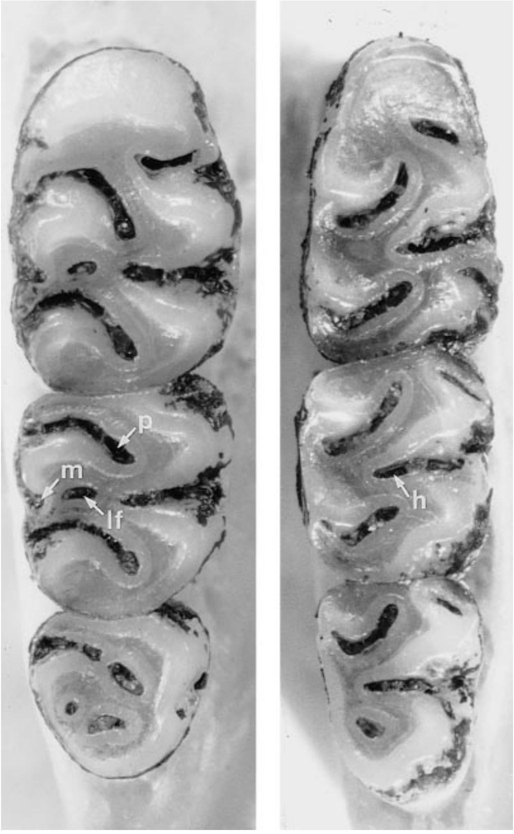

Fig. 119. Occlusal views of right upper and lower molar rows from the neotype (UMMZ 133811) of *Mus megacephalus* Fischer (1814). ×20. Abbreviations: **h**, hypoflexid; **lf**, labial fossette; **m**, mesoflexus; **p**, paraflexus.

coat, which is dark grayish brown over the upperparts and dark gray sparsely spotted with white over the underparts; the fur is very soft, short (up to 5 mm), and feels dense to the touch. Two specimens (UMMZ 133808 and 133810) are in mostly juvenile pelage but have adult fur on the venter and along sides of the body. Finally, UMMZ 133803 and 133805 are covered by mostly adult fur that is nearly completely grown out, but juvenile pelage remains along midline from head to rump. These specimens appear tricolored: grayish white on the venters, tawny along the sides, and dark grayish brown on the dorsum. We examined only the skulls of four other young animals, UMMZ 137009–137012.

Philip Myers (personal commun., letter in AMNH Mammalogy Archives) generously provided information about the habitat in which the neotype was captured. The specimen was trapped during a cold and rainy night ‘‘on a ranch belonging to Ed Borjesson, near the town of Curuguaty, in a region that is characterized by low hills covered with mostly second-growth subtropical forest, and valleys with wet, grassy marshes called cañadones. . . . Soils tend to be clayey. . . .’’ ‘‘According to my notes,’’ wrote Myers, the ‘‘ ‘forest is very low and scrubby, few trees over 40 or 50 ft. Lots of vines, some orchids but not nearly as many as in higher forest. Floor is fairly closed, with many bromeliads, shrubs, and vines.’ ’’ All examples of *O. megacephalus* captured by Myers came from the forest interior, not along the edges (a different ecotonal habitat where *O. subflavus* was regularly encountered), and were taken in traps placed both on the forest floor and up to 8 or 9 ft above ground on vines and low tree branches. A few examples of *O. ratticeps* were also taken in the forest about 20 ft from the forest edge. In addition to the *Oryzomys*, Myers and his field crew caught other rodents (*Oligoryzomys microtis* and *O. nigripes*, *Nectomys squamipes*, *Akodon cursor*, and *Oxymycterus delator*), marsupials (*Lutreolina*, *Didelphis albiventris* and *D. aurita*, *Gracilinanus agilis*, *Caluromys lanatus*, *Chironectes*, *Metachirus*, *Philander*), bats, and species of larger mammals (which included coatis, foxes, jaguarundi, *Sylvilagus*, and *Mazama*).

On the vegetation map of Hueck and Seibert (1981), the region in which Curuguaty lies was identified as ‘‘Bosques subtropicales deciduos y mesofiticos del Brasil oriental y meridional, en parte con alta proporción de especies siempreverdes.’’ Acevedo et al. (1990: 28–29) characterized the area as ‘‘Ecorregión SELVA CENTRAL,’’ which is ‘‘típicamente una selva sub-tropical . . ., también descripta como bosque húmedo templado cálido por Holdridge . . ., presenta una combinación de bosque alto en su mayoría, intercalándose con praderas naturales, en menor grado. . . .’’ The topography, noted Acevedo et al., ‘‘varía desde ondulada hasta muy accidentada, con una variación altitudinal entre los 86 metros en las cercanías de Yuty y los 516 metros en el Cerro Mbo-

Fig. 120. Dorsal views of crania from types in the *Oryzomys megacephalus* complex. **A**, holotype of *O. perenensis* Allen (BMNH 0.7.7.25, adult male), Perené, Perú; **B**, holotype of *O. modestus* Allen (AMNH 14734, young adult female), Campo Alegre, Venezuela; **C**, holotype of *O. velutinus* Allen and Chapman (AMNH 5949/4679, adult male), Trinidad; **D**, holotype of *O. goeldi* Thomas (BMNH 97.4.1.1, young adult female), Itaituba, Rio Tapajóz, Brazil; **E**, holotype of *O. oniscus* Thomas (BMNH 3.10.1.42, adult male), Sao Laurenço da Mata, Brazil; **F**, lectotype of *Mus laticeps* (UZM 266, adult female), Lagoa Santa, Brazil. ×2. Cranial and dental measurements are listed in table 47. The lectotype of *laticeps*, also portrayed in figure 122, is repeated here to compare directly with the crania of *perenensis* and *oniscus*, the other two holotypes representing large-bodied populations within the *O. megacephalus* complex.

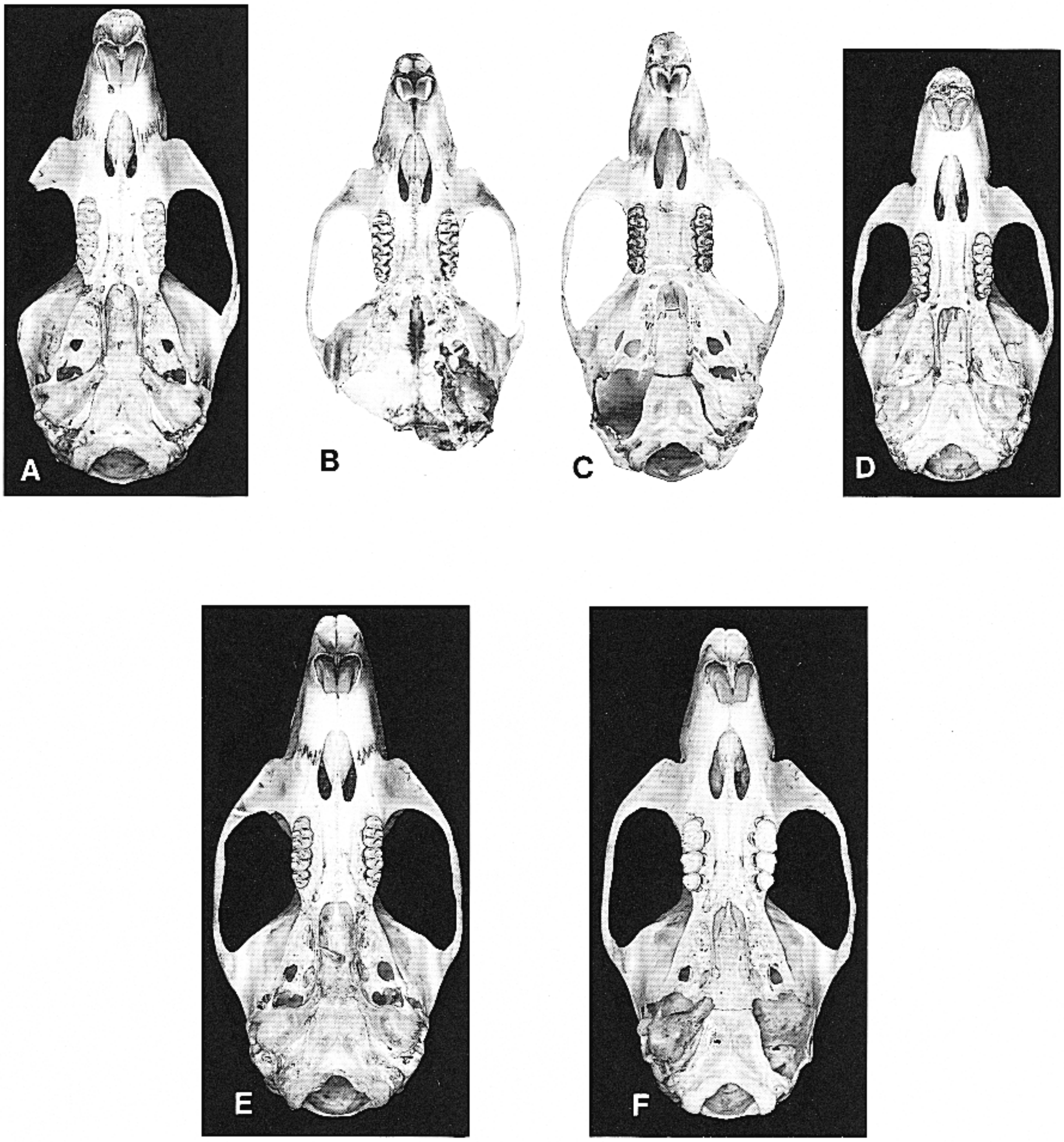

Fig. 121. Ventral views of the same crania shown in figure 120. **A**, *O. perenensis*; **B**, *O. modestus*; **C**, *O. velutinus*; **D**, *O. goeldi*; **E**, *O. oniscus*; **F**, *M. laticeps*. ×2.

cayá,'' and the soils ''son rojo-amarillentos podsólicos con integrados a latosoles, arenosos a lómico-arenosos de color rojo, áridos en la superficie y con baja fertilidad, pero con buenas caracteristicas físicas.''

Allocation of *capito*: After Fischer's *megacephalus*, the next available scientific name for Azara's ''Rat à grosse tête'' is *capito*, validated by Olfers in 1818 (p. 209), but first used by Illiger in 1815. Although ''there is little doubt that Illiger's names referred to Azara's descriptions . . . the author did not make a clear statement thereon and his names must be considered 'nomina nuda' '' (Langguth, 1966). ''The majority of Illiger's manuscript names, or *nomina nuda*, for

South American mammals were validated in 1818 by Olfers'' (Hershkovitz, 1959).

ALLOCATION OF *CEPHALOTES*: This is the third name based on Azara's ''Rat second, ou Rat à grosse tête'' and was coined by Desmarest in 1819 (p. 63). Although Desmarest's names have been accorded the widest recognition (Langguth, 1966; also see Tate, 1932a: 2), his *cephalotes* is a junior objective synonym of *Mus megacephalus* (Fischer, 1814).

ALLOCATION OF *VELUTINUS*: This form was named and described as a species by Allen and Chapman in 1893 (p. 214). The holotype (AMNH 5949/4679) is an adult male and was collected April 16, 1893 by F. M. Chapman at Princestown, Trinidad (see table 1). The skin and skull (figs. 120, 121) are in good condition. Allen and Chapman provided a lengthy description of pelage coloration and some cranial and dental measurements, but contributed no diagnostic characters (certainly none that would ally it with the *O. megacephalus* complex). We examined the specimen (cranial and dental measurements are listed in table 47) and can report that the specimen is characterized by the traits enumerated in the diagnosis and is an example of the smaller bodied populations of the species we are calling *O. megacephalus* from Trinidad and the Guiana Region.

ALLOCATION OF *GOELDI*: This taxon was named and described by Thomas (1897: 494) four years after the published description of *velutinus*. The holotype is a young adult female (BMNH 97.4.1.1) obtained from Itaituba, on the Rio Tapajós in Pará, Brazil (see table 1), and was given to the British Museum by E. A. Goeldi. The specimen had been preserved in fluid, but later the skull (figs. 120, 121) was extracted and the body converted into a study skin. Thomas characterized *goeldi* as ''Allied to *O. laticeps*, Lund, with some specimens of which it agrees closely in colour and proportions, but much smaller in actual size.'' Thomas's description (p. 494) points to a member of the *O. capito* complex:

> Fur rather short, close, and straight, 6 or 7 millim. long on the posterior back.
>
> General colour dull brown, tinged with dark buff, which is clearer on the flanks. Belly greyish white, well defined, the bases of the hairs slaty grey, the tips white or buffy white, Ears of medium length, thinly haired, brown. Hands and feet dull whitish; the metapodials and digits alike. Tail rather longer than the head and body, slender, very thinly haired; pale brown above and below.
>
> Skull very similar to that of *O. laticeps*, apart from its smaller size.

The small size of the holotype of *goeldi* is impressive (cranial and dental measurements are listed in table 47). The dimensions reflect its young age as well as the small body size that characterizes populations of *O. megacephalus* from the central portion of the Amazon Basin in eastern Pará. In addition to the holotype, our sample of that population comes from the area south of Itaituba between there and Jacaréacanga (locality 39, ''Pará-2'' in table 1). Variation in cranial dimensions falls within that characterizing the samples of small-bodied *O. megacephalus* from the Guiana Region, central and eastern Brazil, and eastern Paraguay (figs. 4, 5).

ALLOCATION OF *MODESTUS*: Named and described by Allen in 1899 (p. 212), this taxon is based on the holotype and is a young adult female (AMNH 14734) collected November 20, 1898 by F. W. Urich at Campo Alegre, 3000 ft (915 m), in Estado de Sucre, Venezuela (''5 km N of San Antonio . . . and 3 km E of Río Cocollar . . . on northern slope of eastern coastal range,'' Paynter, 1982: 26, who also provided these coordinates, 10°10′N/63°45′W). The stuffed skin is undamaged but the posterior portion of the braincase is missing (figs. 120, 121). Allen's description is not helpful in establishing the identity of *modestus*; basically, he described coloration of the skin and feet and provided cranial and dental measurements. He noted that *modestus* ''appears to be very distinct from any previously described species.'' The holotype (measurements are listed in table 47) is clearly an example of *O. megacephalus* from the populations in eastern Venezuela and the Guiana Region.

ALLOCATION OF *PERENENSIS*: This taxon was named and described by Allen in 1901 (p. 406). The holotype (BMNH 0.7.7.25) is an adult male collected April 11, 1900 by P. O. Simons from Perené, 800 m, Departamento de Junín, Perú. The skull is intact (figs. 120, 121) and the skin is in good condition. Allen characterized *perenensis* as ''very sim-

TABLE 47

Measurements (mm), Weight (g), Age, and Sex of Type Specimens Identified as Examples of Either *Oryzomys megacephalus* or *Oryzomys laticeps*

	O. megacephalus					*O. laticeps*	
	megacephalus[a] UMMZ 133811	*velutinus*[b] AMNH 5949/4679	*goeldi*[b] BMNH 97.4.1.1	*modestus*[b] AMNH 14734	*perenensis*[b] BMNH 0.7.7.25	*laticeps*[c] UZM 266	*oniscus*[b] BMNH 3.10.1.42
Age	Adult	Adult	Young adult	Young adult	Adult	Adult	Adult
Sex	Male	Male	Female	Female	Male	Female	Male
LHB	131	132	96	120	125	—	140
LT	119	118	104	100	112	—	145
LHF	31	26	26	28	31	—	33
LE	20	17	15	20	22	—	24
WT	57	—	—	—	—	—	—
ONL	31.3	32.0	29.4	—	34.3	34.3	36.0
ZB	16.2	15.6	14.4	—	17.5	17.7	17.8
IB	5.2	5.3	5.0	5.0	5.2	5.4	5.4
LR	9.8	9.8	9.6	9.1	10.8	?	11.7
BR	6.3	5.6	6.0	5.7	6.7	7.0	6.9
LB	12.1	11.8	11.1	—	12.8	—	12.6
HBC	8.6	8.5	8.1	—	9.2	?	9.1
BZP	3.5	2.9	2.8	3.3	3.7	3.8	3.7
LD	7.9	7.8	7.4	7.9	8.5	?	8.7
LBP	7.3	6.5	6.1	6.5	7.1	7.1	7.1
PPL	10.7	11.1	9.5	—	11.2	?	11.9
LIF	3.8	4.2	4.9	4.8	4.8	?	4.9
BIF	2.2	2.3	2.4	2.3	2.4	?	2.8
CLM1–3	4.8	4.7	4.6	4.7	5.3	5.2	5.0
BM1	1.5	1.3	1.4	1.4	1.5	?	1.4

[a] Neotype.

[b] Holotype. External measurements are those listed in the original published descriptions cited in the synonymies.

[c] Lectotype.

ilar in coloration, texture of pelage, size, and proportions to *O. magdalenae* Allen, but with the skull much broader and the dentition much heavier." He ended the account of *perenensis* (p. 407) by noting that "Externally this form is not readily distinguished from *O. magdalenae,* but the two are easily separable on comparison of the skulls. Both are apparently geographical forms of *O. laticeps.*" The holotype of *magdalenae* is actually an example of *O. talamancae* (see Musser and Williams, 1985: 13). The broader skull and heavier dentition of *perenensis* relative to that of *magdalenae* mirror a primary size contrast between the two species: samples of *O. megacephalus* have, on average, significantly larger skulls, longer maxillary toothrows, and wider molars than do samples of *O. talamancae* (table 35). The holotype of *perenensis* is a typical example from the large-bodied populations of *O. megacephalus* living at the western margins of the Amazon Basin in Perú (see figs. 4 and 5 and the measurements listed in appendix A).

ORYZOMYS LATICEPS

Mus laticeps Lund (1840 preprint of Lund, 1841: 279). TYPE LOCALITY: Brazil, Estado de Minas Gerais, Lagoa Santa, valley of the Rio das Velhas. LECTOTYPE: UZM 266 (skin, skeleton, and skull, fig. 122; measurements listed in table 47), an adult female collected by P. W. Lund.

Calomys saltator Winge (1887: 48). A renaming of Lund's *Mus laticeps*; the name attaches to the lectotype, UZM 266.

Oryzomys oniscus Thomas (1904: 142). TYPE LOCALITY: Brazil, Estado do Pernambuco, São Lourenço da Mata, 50 m (sample 44 in table 1). HOLOTYPE: BMNH 3.10.1.42 (skin and skull, figs. 120, 121; measurements listed in table 47), an adult male collected July 23, 1903 by A. Robert.

EMENDED DIAGNOSIS: An oryzomyine that can be distinguished from eastern Amazonia populations of *O. megacephalus* by its greater external, cranial, and dental dimensions and by its 2*n* of 52; apparently *O. laticeps* can be separated from western Amazonia populations of *O. megacephalus* only by molecular data (fig. 6).

DISTRIBUTION: Atlantic Forest region of eastern Brazil.

DESIGNATION OF LECTOTYPE FOR *LATICEPS*: In 1840 (preprint of 1841 text), Lund described the rodents obtained at Lagoa Santa (19°38′S/43°53′W) in the valley of the Rio das Velhas in Minas Gerais, Brazil. He applied existing names to some of the species, but described others as new. Lund arranged the accounts into two groups, one containing species ''in which the tails are longer than bodies,'' and the other in which tails are shorter; *Mus laticeps* was included in the latter. Here is a translation (by E. Brothers) of Lund's short description of *Mus laticeps* (p. 279; the original in Danish is reproduced in appendix J):

> The second group, where tails are shorter than bodies, contains species not as big as the first. The first species is *Mus laticeps*, 10″ 5‴ long, of which the body is 5″ 5‴, tail is 5″, characterized by its broad and high head, large ears, protruding eyes, and very delicate tail. The color above is light ash-gray with strong intermixing of rust-yellow; the venter is pure white.[9]

During November 1978, Gardner visited Copenhagen and studied the documents and specimens related to material collected by Lund and others at Lagoa Santa as well as Winge's writings (1887) about the fauna in the Lagoa Santa region. Gardner located a catalog sheet in Winge's handwriting associated with the skin of UZM 266 identifying it as ''Lund's 1ste Expl. of 'Mus laticeps'.'' The skin is matched with a skull and partial skeleton, both labeled L14. The skeleton has a label stating, also in Winge's handwriting, ''Lund's 1ste Expl. of Mus laticeps. Vist tet skind Nr. 266''. The same skull and skeleton were entered in another catalog on ''18/10/1884'' and given the number 46. No date of collection is indicated. The skin, skull, and skeleton had been identified by Winge as *Calomys saltator*. The skull had also been labeled ''Type of *Mus laticeps*'' by Alfredo Langguth during his visit to Copenhagen in 1966 (Langguth, 1975: 50). Fritz W. Braestrup told Gardner that all of Lund's specimens designated ''1ste Expl.'' by Winge are considered to be types in the Copenhagen Museum.

The skull of UZM 266 is an adult with worn molars in which the occlusal patterns are barely discernible. The cranium is intact except for a missing left auditory bulla, broken pterygoids, and perforated rostrum above the nasal capsules (fig. 122). The short incisive foramina have the outline of a teardrop, each second upper molar lacks an enamel island (medial fossette), and no trace of either a squamosoalisphenoid groove or sphenofrontal foramen exists. No sex is indicated on any label, but abdominal and inguinal mammae are easily discernible on the skin, and pectoral mammae could be detected with a little effort. The body of the skin is stuffed, but legs and tail are not. Ears are scantily haired and the same color as the dorsum, which is brown. The venter is white with gray showing through. Dusky coloration of lower legs extends to heels, and the remainders of front and hind feet are white dorsally. No measurements are associated with the skin or indicated in the catalog.

Lund did not designate a holotype or indicate the number of specimens upon which he based his description. We designate the skin, skeleton, and skull of UZM 266 (all these elements also bear the notation L14 and 46), an adult female, as lectotype of *Mus laticeps* Lund (1840). We justify our action by the following explanation. The only specimens of *laticeps* in Copenhagen are UZM 266, 267 (skin only), 268 (skin and skull), 269 (skin and skull), and 389 (skull and body in fluid). Numbers 267–269 and 389 had been collected at Lagoa Santa by the Danish biologist J. Reinhardt sometime during the period 1849–1851 and in 1855. None of these four can be considered syntypes because they were collected after 1840, the publication date of Lund's description of *laticeps*. The skin and skeleton of UZM 266, ''Lund's 1ste Expl. of Mus laticeps,'' is the only specimen we know of that is associable with Lund's original description. However, Winge (1887: 151; see following discussion under allocation of *saltator*) noted that

Fig. 122. Cranium and left dentary of the lectotype (UZM 266) of *Mus laticeps* Lund, an adult female from Lagoa Santa, Brazil. Some measurements are listed in table 47. Additional information is provided in text. ×3.

''Lund's original specimens of *laticeps* are both of the same species,'' indicating that Lund had at least two specimens at the time he wrote the description of *laticeps*. Winge's statement suggests that UZM 266 can be considered a syntype, leading us to apply the requirement of recommendation 73F (p. 151) in the *International Code of Zoological Nomenclature* (1985 edition):

> Where no holotype was designated and where it is possible that a nominal species-group taxon was based on more than one specimen, an author should proceed as though syntypes may exist and, where appropriate, should designate a lectotype rather than assume a holotype.

ALLOCATION OF *SALTATOR*: In 1887 (p. 48), Winge described a new species, *Calomys saltator*[10] (the following passage was extracted from S. Hoslett's translation [MS in library of R. S. Voss, AMNH, Mammalogy]; Danish version is reproduced in appendix K):

> Occurring at Lagoa Santa (brought home is 1 in spirits, 1 skeleton, 4 skins), but up to the present found not with complete assurity in owl pellets of Recent time or found fossilized.
>
> Its closest relative is most clearly *C. longicaudatus* and *C. plebejus*; but it has distinguishable individuality.
>
> From *C. laticeps* it deviates in the following:
>
> Externally. Ears are large; Lappet on the anterior border of the ear hardly visible; *Antitragus* almost not projecting. The hands considerably longer and smaller; the friction pads large and with projecting ends; the hide between the friction pads ''scaly-gravelly''; all the whorls on the under side of the fingers clear; 7, 7, 7, 6. Foot longer and smaller, the three middle toes especially longer; the friction pads strikingly pointed; the hide between the friction pads scaly-gravelly; the whorls on the ventral side of the toes complete: 4, 9, 10, 9, 6.
>
> Fur of the ear for the most part very thinner, with only short scattered hairs so that the naked hide seems to be considerable; only a sharply bounded piece of *Helix* anteriorly is compactly clothed with the same soft fur as the temples. The body fur is much shorter and softer, the individual over-fur hairs finer. On the whole upper side and also on the head there are a few of the dark hairs, and the yellowish hair approaches a tawny color; seen from a distance, the upper side is therefore a uniform tawny. . . .
>
> Teeth. The lower incisor produces by its posterior end almost no projection on the outside of the mandible. Otherwise, there can be discerned almost no real difference.
>
> Skull. The cranium is smaller in proportion to the face. Forehead anteriorly a little more noticeably hollowed out. No *Prc. supraorbitalis*. Orbital border of the frontal sharp. *Foramen opticum* considerably smaller, partly because somewhat ossified to the membrane, which otherwise partly fills it up. No fontanelle in the side wall of the nasal passage towards *Fissura orbitalis*. *Prc. posttympanicus* is bifurcated posteriorly; but the notch is not short. *Foramen incisivum* much shorter, extending less far forward and less far backwards. Most frequently only a faint indication of the pit about the posterior *Foramen palatinum*. Bullae uncommonly small and flat, covering less of the *Foramen lacerum anterius*. A small fontanelle in *Pars mastoidea*. *Tegmen tympani* a little longer, touching *Squama*, but yet does lie plate-like outside on the posterior border of *Squama*. The mandible has no distinguishable projecting bump from the posterior end of the incisors. *Prc. coronoideus* has a more inclined anterior border. Parietal bone has almost no plate on the lateral side of the cranium.

A few postcranial features were noted, and measurements were listed of the skin, cranium and mandible, and dentitions.

In this description of *saltator*, Winge described the ''1st Expl'' of Lund's *Mus laticeps*, and in doing so simply renamed Lund's taxon as *Calomys saltator*. A portion of footnote 5 at the back of Winge's report on the rodents from Lagoa Santa provides insight to Winge's reason (Winge, 1887: 151, part 10 of footnote 5; translated from Danish by E. Brothers; Danish version is reproduced in appendix L):

> *Calomys saltator* is a new name given to one of the two species that have been confused under the name *Hesperomys laticeps* Lund. Lund's original specimens of *laticeps* are both of the same species, here called *saltator*; but Lund did not have a complete grasp of the species. Reinhardt, who also collected mice during his time with Lund in Lagoa Santa, and who had supposedly conferred with Lund about names, used the name *laticeps* on labels for another species, a color variety of *H. vulpinus* Lund. Burmeister also used *laticeps* for *vulpinus* Lund, but in this instance, I cannot really make sense of Burmeister's description because too little is characterized. Giebel (Beitr. Oseteol. Nageth., pl. V, f. 6) has illustrated the skull of Burmeister's specimen of *laticeps* from Lagoa Santa (Giebel: Zeitschr. ges. Naturw., Bd. 28, 1866; p. 120); to be sure, the illustration is very inexact and under the name *H. subflavus* Wagner, although it represents Lund's ''*vulpinus*.'' (Burmeister considers Wagner's *H. subflavus* to be the same as ''*laticeps*''; but this is not definitive and the issue cannot be settled without examining the types.) The name *vulpinus* Lund cannot contain it, because that

---

[10] Explaining Winge's concept of *Calomys*, Voss (1993: 32) noted that ''Whereas *Calomys* (with type species *C. bimaculatus*) is nowadays understood to contain only tetralophodont phyllotines, Winge (1887) used the name for pentalophodont species currently referred to *Delomys*, *Oligoryzomys*, and *Oryzomys*.''

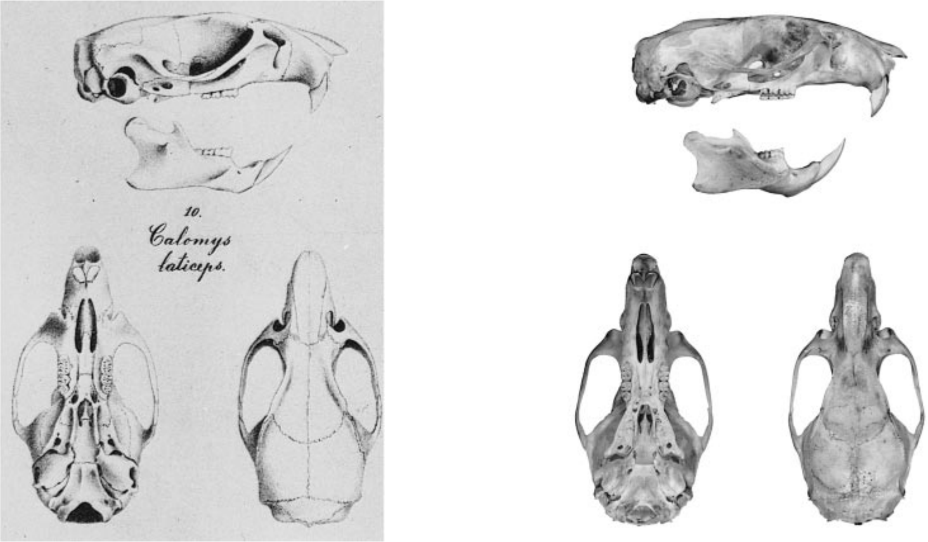

Fig. 123. Winge's (1887: pl. 3, fig. 10) cranial drawing of ''*Calomys laticeps*'' compared with an example of *Oryzomys subflavus* (AMNH 134660) from Anápolis, Estado de Goiás, Brazil. Winge had incorrectly associated Lund's *Mus laticeps* with specimens from Lagoa Santa that have the characteristics of the species currently known as *Oryzomys subflavus*. Winge's ''*laticeps*'' and *subflavus* share long incisive foramina, a short palatal bridge, and prominent shelves overhanging the postorbital region, all of which are diagnostic for *O. subflavus*. The actual specimens that Lund had described as *Mus laticeps* are examples of the same species from Lagoa Santa that Winge later described as ''*Calomys saltator*'' (see fig. 124 on opposite page). We discuss these identifications in the text.

> name was used earlier for another species, *H. vulpinus* Licht. In this situation, it is proper to allow the name *laticeps* to remain with one species, that which fits Giebel's illustrations, and to give the new name, which is necessary, to the other of the two confused species.
>
> What Thomas (Proc. Zool. Soc. 84) considers as ''*Hesperomys* (*Oryzomys*) *laticeps* Lund'' is not apparent.

In 1854, Burmeister (pp. 171–172) had described a rat from Lagoa Santa under the name ''Hesperomys laticeps *Lund*'' in a subsection of *Hesperomys* titled *Calomys*. He considered Lund's name to also apply to Wagner's (1842) *Hesperomys subflavus*, which Burmeister listed as a synonym of *laticeps*. Below is a translation (made by E. Brothers; his notes are in brackets) of Burmeister's description (the original in German is reproduced in appendix M):

> Upperparts light gold-yellow, strongly mixed with black-brown, nose and forehead grayer; below pale [buff/dun/cream]-yellow, with gray showing through. Ears very large. Tail as long as the body, each is 5½–6″.—
>
> The form is the same as the previous species [in that previous account, Burmeister had described *H. leucogaster*], just as full and soft-haired, but somewhat smaller, the tail shorter, the ears larger, the color tones lighter. Front of head from the nose to behind the eyes white-gray, mixed with many black hairs; from there on the entire dorsum is light yellow-gray, a mixture of yellow and black guard hairs, beneath which lie individual longer hairs [bristles] with their white tips; all of the innermost hairs are slate gray. Throat white, the sides at the cheeks [buff/dun/cream]-yellow, the chest to the forelegs yellowish, from there behind grayish. The middle of the belly and the points white, yellowish at the edges, the color more vibrant at the [thigh-joint] to the edge of the rump and on the [belly-side]. Tail thick-haired, upper side brown, underneath more yellowish. Ears large, broad, rounded, gray-black-haired, inside with yellowish guard hairs, particularly at the perimeters. Mystacials abundant, extending somewhat past the ear; most are black-brown with whitish tips. Lips and paws white. The fore- and hindlimbs are colored as the dorsum, only duller, the footpads are naked and flesh-colored; the incisors are light yellow in front. – Total length 11–12″, head and body 5½–6″:, tail 6″, head up to the ear 15‴ [see footnote 9], inside of ear 8‴, hind foot 14‴.—from Lagoa Santa.
>
> note: Dr. Lund's work on the mice from the same area (op. cit.) includes a brief definition of Mus laticeps which fits with this description, but the dimensions given are nevertheless 1½″ shorter in the body and tail. I have both skins lying in front of me and

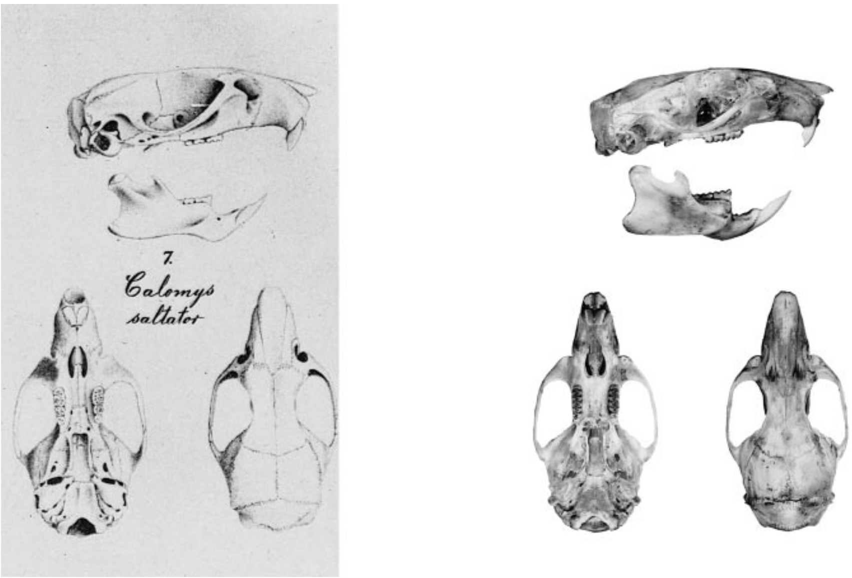

Fig. 124. Winge's (1887: pl. 3, fig. 7) skull drawing of ''*Calomys saltator*'' contrasted with an example of *Oryzomys laticeps* (USNM 545056) from the Atlantic Forest at Ilhéus, Estado da Bahia, Brazil. Winge's ''*saltator*'' is based on the lectotype of *Mus laticeps* Lund. The specimen Winge illustrated is not the one we selected as lectotype (fig. 122), but is an example of true *O. laticeps*. The specimen figured in Winge's drawing, the one from Bahia, and the lectotype all possess short and wide incisive foramina, a long bony palate, and smooth dorsolateral margins of the interorbit—traits characteristic of *O. laticeps* and its close relative *O. megacephalus*. We elaborate on Winge's misguided renaming of *laticeps* in the text.

> the smaller has a relatively somewhat longer tail; both are males. Wagner's work is knowledgeable and leaves no doubt that his species shares the same identity as mine. -– Closely related is Azara's Cola igual al Cuerpo [tail equal to the body] (Quadrup. II. 87. No. 87.—Trad. franc. II. 82.—Mus cephalotes *Desm*. Mamm. 305.—*Brants* Muiz. 144) but it is smaller (body 4″, tail 4″) and lighter gray, mottled with red-brown, white venter.

Burmeister's portrayal generally fits the species currently known as *Oryzomys subflavus*, except for the white paws (buffy in *O. subflavus*) and nearly equal lengths of tail and body (tail is much longer relative to body in *O. subflavus*; see tables 37, 51). Alternatively, his description may just as readily apply to two other oryzomyine species that we identify in our report as *O. laticeps* and *O. russatus*. We are, however, inclined to accept his account as a redescription, under the name *laticeps*, of Wagner's *subflavus* because Burmeister did note that his specimen displayed the ''form'' of *leucogaster*; this is the *leucogaster* originally described by Wagner (1845), a large-bodied and long-tailed species currently known as *Oryzomys ratticeps* (see our account below of *O. russatus*) that is larger than, but morphologically very similar to, *O. subflavus*. Moreover, Winge mentioned in his footnote (see our translation above) that Burmeister considered Lund's *laticeps* and *vulpinus* to be the same, and that the skull from the animal Burmeister described as *laticeps*, which Giebel (1857) illustrated, is a *vulpinus*. Lund (1840) did describe *Mus vulpinus*, and the lectotype is an example of what is currently known as *O. subflavus*, an identity we discuss below in the section on the *Oryzomys subflavus* Group. Furthermore, we examined Giebel's report (1857: pl.5, fig. 6) and agree with Winge that while the drawing is ''inexact,'' it does represent an example of Lund's *vulpinus*, or *O. subflavus* as it is known today.

Winge's solution to the problem he described in the footnote was idiosyncratic. Burmeister incorrectly regarded his material to be the same species as that represented by the series Lund had described under the name *laticeps*; however, the specimen Burmeister described was an example of the species Lund had earlier described as *vulpinus*. Instead of merely correcting Burmeister's misidentification, Winge decided to retain the name *laticeps* for the species represented by the specimen Burmeister had described and Giebel had illustrated—which is what Winge knew as *vulpinus* and what we call *subflavus*—and then to redescribe Lund's true *Mus laticeps* under a new name, *Calomys saltator* (an action Trouessart [1898: 525 and 1904: 420] must have recognized because he listed *saltator* as a synonym of *Oryzomys laticeps* Lund). Winge's rendering of ''*Calomys laticeps*'' (fig. 123) unquestionably portrayed a skull of *O. subflavus* and his labeling plainly indicated it to be the species he wrongly associated with Lund's *laticeps* (Trouessart's [1904: 421] perception was again astute because he listed ''*laticeps*, Winge (nec Lund)'' in his synonymy of *Oryzomys subflavus*).

Winge's illustration of the cranium and right dentary of ''*Calomys saltator*'' (fig. 124) is an adult example that resembles *Oryzomys megacephalus* and *O. laticeps* (it is not UZM 266, the specimen we designated lectotype of *laticeps*). Gardner noted that in addition to UZM 266, ''Lund's 1ste Expl. of Mus laticeps,'' Winge had before him the skin of UZM 267, the skins and skulls of UZM 268 and 269, and the skull of UZM 389 (as well as the body in fluid) when he named *saltator* (which would correspond to the material Winge [1887: 48] noted ''brought home is 1 in spirits, 1 skeleton, 4 skins''). The five specimens are all examples of the same species—not *O. subflavus*, but the real *O. laticeps*, a species morphologically closely allied to *O. megacephalus*. Selected measurements of the lectotype of *O. laticeps* along with UZM 268, 269, and 369 are listed in table 5. We attach the name *Calomys saltator* (Winge, 1887) to UZM 266, the lectotype of *Mus laticeps* (Lund, 1840); article 72e of the *International Code of Zoological Nomenclature* (1985 edition) is clear in this circumstance:

> If an author proposes a new species-group name expressly as a replacement for a prior one, both have the same name-bearing type, despite any simultaneous application of the replacement name to particular specimens or any contrary designation of type, or any different taxonomic usage of the replacement name.

Winge's *saltator* is an objective junior synonym of Lund's *laticeps*.

ALLOCATION OF *ONISCUS*: This form, named and described by Thomas in 1904 (p. 142), is apparently also a synonym of *O. laticeps*. The holotype (BMNH 3.10.1.42) is an adult male collected July 23, 1903 by A. Robert at São Lorenço da Mata [10 km WNW Recife], 50 m, near ''Pernambuco'' [Recife] in Estado do Pernambuco, Brazil. Thomas characterized *oniscus* as ''A medium-sized species allied to *O. intermedius* and *O. laticeps*'' and provided this description (p. 142):

> Size about as in *O. intermedius*, therefore larger than in *O. laticeps*. Fur close and rather short; hairs of back barely 10 mm. in length. General colour of upper surface dark greyish tinged with buffy, the resulting tone being rather paler than Ridgway's ''bistre'' and very near that of certain of the darker forms of the *laticeps* group, e.g. *O. perenensis*, Allen. Median area of back noticeably darker than rest. Sides rather, but not conspicuously, more buffy. Whole of under surface and inner sides of limbs greyish white . . ., the bases of the hairs slaty, the tips white. Line of demarcation on sides fairly well defined. Head like body; muzzle rather darker, with dark rims round the eyes. Ears rather large, thinly haired, greyish brown. Outer surface of arms and legs drab-grey; hands and feet pure white. Tail approximately equal in length to the head and body, very finely scaled, practically naked; greyish brown, rather paler for its proximal third below.
>
> Skull closely similar in size and shape to that of *O. intermedius*, therefore decidedly larger than in *O. laticeps*; the palatal foramina are, however, rather shorter than in the former, though not so short as in the latter, and are more widely open. The supraorbital edges are squared or finely beaded, but are without overhanging ledges.

Thomas concluded his account of *oniscus* by proclaiming:

> This *Oryzomys* is readily distinguished from any species hitherto known. In its colour it is remarkably like some of the forms of the *O. laticeps* group, but is separable from them by its much larger skull and longer palatine foramina. In some of the specimens the darker dorsal area is so marked as to suggest an affinity with *O. sublineatus*, Thos., but the hind feet in that species are conspicuously shorter.
>
> From *O. physodes*, Licht. (Rio Janeiro and Espirito Santo), *O. lamia*, Thos. (Minas Geraes), and *O. intermedius*, Leche (São Paulo to Rio Grande do Sul), of all of which Mr. Robert has obtained specimens, this species is distinguishable by the absence of the rufous or buffy body-colour found in those animals.

Skin and skull of the holotype of *oniscus* are in good condition and represent a population of the *O. megacephalus* group that is characterized by large body size (the cranium is illustrated in figs. 120 and 121; measurements are listed in table 47). Of the taxa with which Thomas compared it, *oniscus* has nothing to do with *sublineatus*, which is a species of *Delomys* (Voss, 1993), or with *physodes* Brandt (not Olfers, 1818). The holotype of *oniscus* differs from examples of *physodes* Brandt, *lamia*, and *intermedius* not only in the chromatic features noted by Thomas but also in cranial and dental traits. Type specimens of *physodes* Brandt, *lamia*, and *intermedius* are examples of *O. russatus*, a member of the *O. nitidus* group (these identities are discussed in the synonymy for *O. russatus*). Long and narrow incisive foramina (figs. 80, 99) combined with a sphenofrontal foramen and squamosoalisphenoid groove (fig. 151) are among the cranial traits characteristic of species in the *O. nitidus* group; second upper molars contain a medial fossette (or enamel island) and lowers are partially bisected by a short hypoflexid (figs. 29–32, 151). In contrast, the holotype of *oniscus* exhibits the diagnostic cranial and dental traits of *O. megacephalus* and *O. laticeps*: relatively short and wide incisive foramina, no sphenofrontal foramen or squamosoalisphenoid groove, no medial fossette on second upper molar, and a deep hypoflexid extending nearly all the way across each second lower molar. The large cranial dimensions recorded for the holotype of *oniscus*, along with its geographic origin in the Atlantic Forest region of Brazil, ally it with *O. laticeps* (see discussion in beginning section of this report).

ORYZOMYS YUNGANUS

Oryzomys yunganus Thomas (1902: 130). TYPE LOCALITY: Bolivia, Departamento de Cochabamba, Charuplaya, 1350 m (locality 59 in gazetteer and fig. 14). HOLOTYPE: BMNH 2.1.1.39 (skin and skull; fig. 125; measurements are listed in table 22), an old adult male collected June 19, 1901 by P. O. Simons.

Fig. 125. Dorsal, ventral, and lateral cranial views of the holotype of *Oryzomys yunganus* Thomas (BMNH 2.1.1.39), an old adult male from Charuplaya, Bolivia. ×2. Measurements are listed in table 22.

EMENDED DIAGNOSIS: An oryzomyine of moderate body size with tail equal to or shorter than length of head and body; upperparts covered by dense, velvety dark fur (brownish tawny to brownish black), underparts dark grayish white; tail monocolored or with ventral basal half unpigmented or mottled; dorsal surfaces of front and hind feet whitish, claws sparsely covered by ungual tufts, plantar surface without hypothenar pad in some specimens (samples from the Guianas and Bolivia); superciliary, genal, and mystacial vibrissae not exceptionally long, extending only to ears; shape of cranium similar to *O. megacephalus*, but zygomatic plate much wider relative to other cranial dimensions, and lengths of bony palate, incisive foramina, and molar row longer relative to occipitonasal length; alisphenoid struts absent; modified cephalic arterial pattern marked by lack of sphenofrontal foramen and squamosoalisphenoid groove, but presence of large stapedial foramen and prominent groove on

Fig. 126. Dorsal views of crania from holotypes associated with *Oryzomys bolivaris*. **A**, *O. bolivaris* Allen (BMNH 99.9.9.27, old adult male), Porvenir, Ecuador; **B**, *O. rivularis* Allen (BMNH 1.1.6.5, adult female), Río Verde, Ecuador; **C**, *O. castaneus* Allen (BMNH 1.3.19.11, adult female), San Javier, Ecuador; **D**, *O. bombycinus* Goldman (USNM 171105, adult male), ''Cerro Azul,'' Panamá; **E**, *O. nitidus alleni* Goldman (AMNH 9631/7971, young adult male), Tuis, Costa Rica. ×2. Measurements listed in table 48. The holotype of *Oryzomys bombycinus orinus*, the only other taxon associated with *O. bolivaris*, was not photographed.

ventral surface of pterygoid plate for infraorbital branch of stapedial artery; posterior margin of dentary shallowly concave between condyloid and angular process (compared with more deeply concave margin of *O. megacephalus*); molars chunky and wide, second upper molar with short paraflexus, labial and medial fossettes present; second lower molar with conspicuous entoflexid, short hypoflexid extending only to medial plane of tooth, fossettid present; chromosomes $2n = 58$ or 60 and FN = 62 or 66 (Perú and western Brazil), $2n = 52–59$ and FN = 64–67 (Surinam).

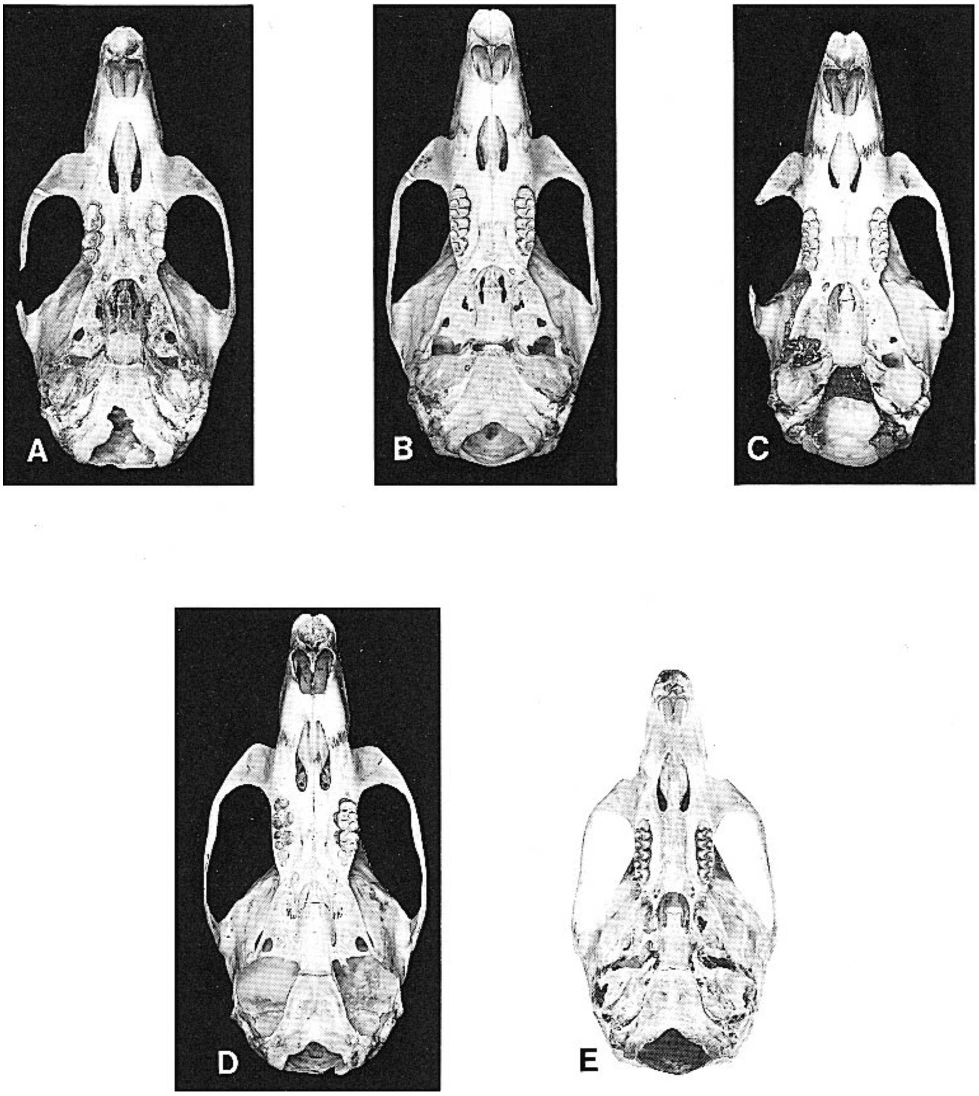

Fig. 127. Ventral views of same crania shown in figure 126 on opposite page. **A**, *O. bolivaris*; **B**, *O. rivularis*; **C**, *O. castaneus*; **D**, *O. bombycinus*; **E**, *O. nitidus alleni*. ×2.

DISTRIBUTION: Tropical evergreen rain forests of Amazonia; documented elevational range extends from near sea level to 2000 m.

REMARKS: Surprisingly, no other published scientific name has been applied to a holotype that represents this species.

The placement of the type locality on the map in figure 14 requires explanation. Perry O. Simons collected at Charuplaya during the latter part of May and first part of June 1901. Thomas (1902: 126) indicated that Charuplaya was ‘‘on the [Río] Sécure, just north of 16° S., comparatively low, with an Amazonian fauna.’’ The position and elevation was, wrote Thomas, ‘‘taken from Mr. Simons’ sketch-map of the district.’’ Charuplaya is not shown on any maps we consulted. Paynter et al. (1975: 12) thought the place to be ‘‘probably below and N of Lagunillas and Choro, possibly on Río Blanco,’’ but in a more recent gazetteer, Paynter (1992: 30) could not locate Charuplaya and noted that ‘‘perhaps this is somehow associated with Río Charopaya, to the S of Inqui-

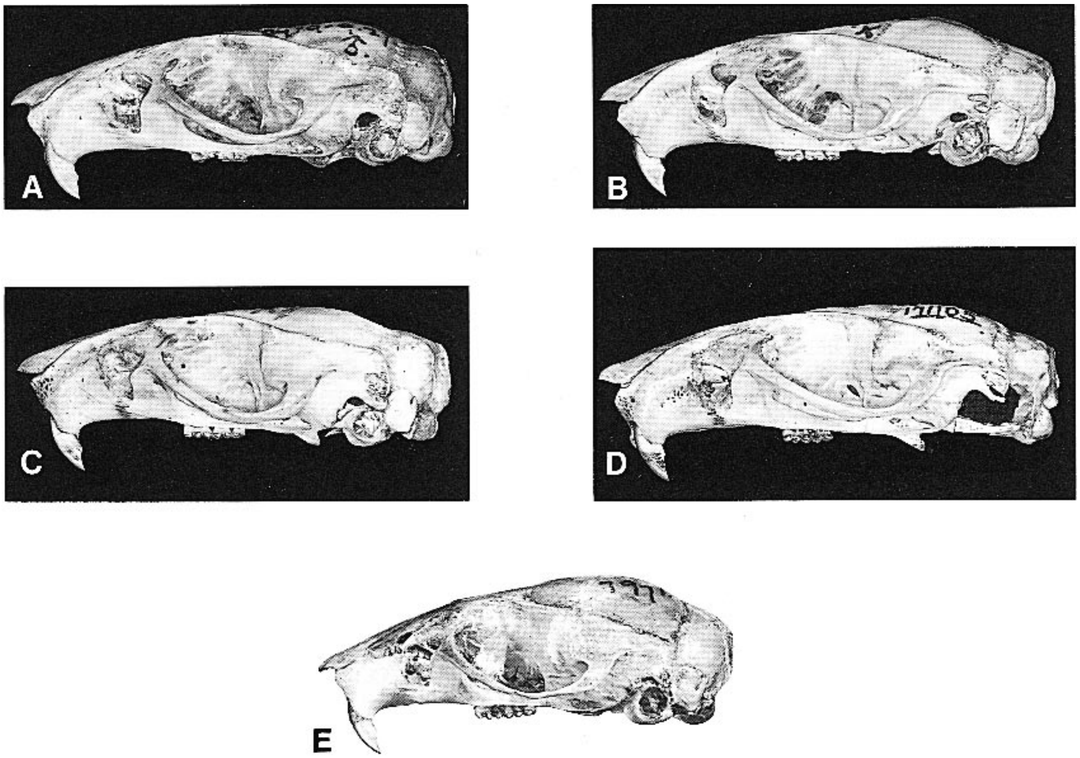

Fig. 128. Lateral views of same crania portrayed in figures 126 and 127. **A**, *O. bolivaris*; **B**, *O. rivularis*; **C**, *O. castaneus*; **D**, *O. bombycinus*; **E**, *O. nitidus alleni*. ×2. The parietal does not extend ventrally past the temporal ridge (see fig. 62) in any of the type specimens; this configuration is diagnostic for *O. bolivaris*.

sivi, as Simons is known to have been in this region about this time.'' Sydney Anderson (1997: 90; personal commun.) thinks Charuplaya is ''probably on the Río Santa Elena rather than the headwaters of the río Sécure, at 1300 to 1400 m, northward of Lagunillas,'' and estimates the coordinates to be 16°36′S/66°37′W. Anderson's determination was influenced by Chubb's (1919: 5) report in which he provided a ''list of the localities where specimens were collected by Simons . . . arranged in chronological order from his diaries.'' Simons was in Cochabamba from April 18 to 24, from where he traveled about 80 km northwest so that by May 5 he was in Choro at 3500 m. From there he journeyed north–northeast to arrive by May 17 in Lagunillas at 3000 m (''Langunillas'' at ''3500 m'' in Chubb's list) in the upper reaches of the valley of the Río Santa Elena. Simons spent the next day (May 18) and from May 27 until the first part of June in Charuplaya, 1300 m. That elevation would place Simons along the Río Santa Elena about 10 km down the river valley north of Langunillas, which seems to Anderson, and to us, the most likely location of Charuplaya, a site that could be reached by walking, or with mules or horses, in the time between May 17 and 18. The headwaters of the Río Sécure at 1300 m, Thomas's (1902) designation, are approximately 100 airline km north of Lagunillas, which would translate into an overland distance too great to have been traversed on foot or with animals between May 17 and 18. We think it likely that Simons confused the upper reaches of the Río Santa Elena, which flows northwestward to join the Río Beni, with the headwaters of the Río Sécure, which flows from west to east and is a tributary of the Río Mamoré. When referencing Simons' map, Thomas (1902: 126) indicated that

Choro was ''on the high paramos north and north-west of Cochabamba, surrounding on the west and south the sources of the Río Sécure, *which flows northward* [our emphasis] to join the Mamoré and ultimately the Amazon.'' That description perfectly reflects the position of Choro relative to the headwaters of the northward-flowing Río Santa Elena. In our attempt to retrace Simons' journey, we used the ''Mapa de la República de Bolivia'' (1:1,000,000; third edition, 1980, Instituto Geográfico Militar, La Paz), graciously loaned by Sydney Anderson.

ORYZOMYS TATEI

Oryzomys tatei Musser, Carleton, Brothers, and Gardner (present report). TYPE LOCALITY: Ecuador, Provincia de Tungurahua, Palmera, 4000 ft (locality 26 in gazetteer and figs. 14, 47). HOLOTYPE: AMNH 67361 (skin and skull, figs. 44, 45; measurements listed in table 22), an adult male collected February 9, 1924 by G.H.H. Tate.

DIAGNOSIS: A large-bodied species related to *Oryzomys yunganus* but with darker upperparts, larger molars (in absolute and relative dimensions), smaller incisive foramina relative to cranial size, and relatively blunt coronoid process on the dentary.

DISTRIBUTION: Known only from Mirador, Palmera, and Mera in the zone of wet evergreen rain forest between 1128 and 1524 m along the eastern Andean foothills of central Ecuador.

ORYZOMYS BOLIVARIS

Oryzomys bolivaris Allen (1901: 405). TYPE LOCALITY: Ecuador, Provincia de Bolívar, Porvenir, 1800 m (locality 36 in gazetteer and fig. 50). HOLOTYPE: BMNH 99.9.9.27 (skin and skull, figs. 126–128; measurements listed in table 48), an old adult male collected March 10, 1899 by P. O. Simons.

Oryzomys castaneus Allen (1901: 406). TYPE LOCALITY: Ecuador, Provincia de Esmeraldas, San Javier, 60 ft (locality 30 in gazetteer and fig. 50). HOLOTYPE: BMNH 1.3.19.11 (skin and skull, figs. 126–128; measurements listed in table 48), an adult female collected July 28, 1900 by G. Flemming and R. Miketta.

Oryzomys rivularis Allen (1901: 407). TYPE LOCALITY: Ecuador, Provincia de Pichincha, Río Verde, 3200 ft (locality 31 in gazetteer and fig. 50). HOLOTYPE: BMNH 1.1.6.5 (skin and skull, figs. 126–128; measurements listed in table 48), an adult female collected November 28, 1899 by R. Miketta.

Oryzomys bombycinus Goldman (1912: 6). TYPE LOCALITY: Panamá, Provincia de Panamá, Cerro Azul, 2500 ft, near headwaters of Río Chágres (locality 19 in gazetteer and fig. 50). HOLOTYPE: USNM 171105 (skin and skull, figs. 126–128; measurements listed in table 48), an adult male collected March 26, 1911 by E. A. Goldman.

Oryzomys nitidus alleni Goldman (1915: 128). TYPE LOCALITY: Costa Rica, Provincia de Cartago, Tuis, about 35 miles E Cartago (locality 12 in gazetteer and fig. 50). HOLOTYPE: AMNH 9631/7971 (skin and skull, figs. 126–128; measurements listed in table 48), a young adult male collected July 15, 1894 by G. K. Cherrie.

Oryzomys bombycinus orinus Pearson (1939: 2). TYPE LOCALITY: Panamá, Provincia de Darién, Mount Pirre, 4700 ft, along the Río Limón (locality 22 in gazetteer and fig. 50). HOLOTYPE: ANSP 19709 (skin and skull; measurements listed in table 48), an old adult male, collected March 12, 1938 by O. P. Pearson.

EMENDED DIAGNOSIS: An oryzomyine of moderate body size with tail more or less equal to length of head and body; upperparts covered with dark (brownish tawny to dark brown) and dense fur, underparts grayish white; tail monocolored or mottled on ventral surface; dorsal surfaces of front and hind feet whitish, claws sparsely covered by ungual tufts, plantar surface with six pads; superciliary, genal, and mystacial vibrissae exceptionally long, extending well beyond posterior margins of ears; cranium elongate, noticeable supraorbital ridges or narrow shelves, parietal does not contribute to side of braincase in form of winglike extension ventral to squamosal–parietal suture; no alisphenoid struts; long incisive foramina and short bony palate; complete cephalic arterial pattern as marked by sphenofrontal foramen and squamosoalisphenoid groove, large stapedial foramen, and prominent groove on ventral surface of pterygoid plate for infraorbital branch of stapedial artery; ascending ramus of dentary broad (compared to *O. talamancae*); second upper molar with long paraflexus and labial fossette, medial fossette absent; second lower molar with deep hypoflexid nearly bisecting occlusal surface of

TABLE 48
Measurements (mm), Age, and Sex of Holotypes Identified as *Oryzomys bolivaris*

	bolivaris BMNH 99.9.9.27	*castaneus* BMNH 1.3.19.11	*rivularis* BMNH 1.1.6.5	*bombycinus* USNM 171105	*alleni* AMNH 9631/7971	*orinus* ANSP 19709
Age	Old adult	Adult	Adult	Adult	Young adult	Old adult
Sex	Male	Female	Female	Male	Male	Male
LHB	125	118	111	125	—	124
LT	100	105	127	127	—	126
LHF[a]	30	29	32	31	—	28
LE	18	19	17	—	—	19
LDF	7	7	8	11	9	12
LMV	46	41	49	49	41	43
LSV	—	40	43	58	45	45
LGV	29	34	36	39	35	45
EPVTR[b]	0	0	0	0	0	0
ONL	30.7	30.1	31.8	31.0	28.1	30.9
ZB	15.3	14.2	15.0	15.0	14.2	15.3
IB	5.3	5.4	5.5	5.2	5.2	5.2
LR	9.7	9.1	9.5	9.3	8.7	9.7
BR	5.6	5.6	5.7	5.3	4.8	5.1
LB	11.8	11.5	12.3	11.4	11.5	11.8
HBC	8.9	—	8.8	8.4	8.8	8.8
BZP	3.1	3.3	3.2	2.8	2.7	3.0
LD	8.1	7.4	7.9	8.0	6.8	8.2
LBP	6.1	6.2	6.6	6.1	5.5	6.4
BBP	5.8	5.9	5.9	5.7	5.3	5.6
PPL	10.5	—	10.9	11.0	9.2	9.8
LIF	4.9	4.3	3.9	4.7	4.4	4.1
BIF	2.4	2.3	2.3	2.4	2.0	2.3
CLM1–3	4.1	4.2	4.6	—	4.2	4.2
BM1	1.2	1.2	1.3	1.3	1.3	1.2

[a] Values obtained by us from measuring stuffed museum skins.

[b] Extent of parietal ventral to temporal ridge; see table 31 and figure 62.

tooth, shallow entoflexid, and no fossettid; chromosomes $2n = 58$ and $FN = 80$.

DISTRIBUTION: Wet and humid lowland and montane evergreen forests in the trans-Andean region from northeastern Honduras through eastern Nicaragua, Costa Rica, Panamá, to Colombia and Ecuador west of the Andes; documented elevational range extends from near sea level to 1485 m.

TYPE LOCALITY OF *BOLIVARIS*: Paynter and Traylor (1977: 53) provided the coordinates 01°05′S/79°39′W for Hacienda Porvenir, where P. O. Simons collected on March 10, 1899 (the day he captured the holotype of *bolivaris*), and indicated the place was in Provincia Bolívar. Paynter (1993: 89), however, could not locate Hacienda Porvenir, but referred to Brown (1941: 842), who had stated that "there is an Hacienda of this name [El Porvenir] belonging to the Cordovez family about a half day's journey west of Hda. Talahua." The latter site, with coordinates 01°21′S/79°04′W, was another place where P. O. Simons collected animals. According to Chubb (1919: 3), Simons was in Provincia Bolívar at Hacienda Talahua on March 1 and had moved to "Povenir," in the same province, by March 10. We cannot find Hacienda Porvenir on maps. Hacienda Talahua is in northern Bolívar and we simply placed the dot on our distribution map (fig. 50) in northern Bolívar west of Talahua, assuming that "a half day's" travel would not have taken Simons beyond the province boundaries.

ALLOCATION OF TAXA: The names *bombycinus, alleni,* and *orinus* have traditionally been associated with the same species (Pine, 1971; Hall, 1981). The older names *bolivaris*, *castaneus*, and *rivularis*, however, have not and we need to explain our identifications of the holotypes upon which these names are based.

Allen (1901) presented all three names in the same report, designating each as a species and diagnosing them primarily by coat color. To Allen (p. 405), *bolivaris* was:

> Above medially dark brown, punctuated with ferruginous, the general effect being what might be called dark chestnut brown; sides lighter, more yellowish brown, becoming gradually paler towards the ventral surface, which is sharply defined and dull white, the fur being plumbeous at base and broadly tipped with soiled white. . . .

The coloration, he thought, resembled members of the *O. magdalenae* group (*magdalenae* is now treated as a synonym of *O. talamancae*), ''but the general effect is much darker and more bordering on dark chestnut than yellowish brown, but from which group it differs in its relatively somewhat shorter tail and very much smaller ears'' (pp. 405–406).

The species *O. castaneus* was described next and Allen characterized its fur as ''above dark reddish brown or light chestnut, paler, more yellowish brown on the sides; below dull whitish or soiled grayish white, the fur being plumbeous at base and broadly tipped with whitish'' (p. 406). Musser and Williams (1985: 14) incorrectly associated *castaneus* with *O. talamancae*.

Oryzomys rivularis was presented on the following page and Allen diagnosed it as ''coloration throughout essentially like *O. bolivaris*, but much larger and with the tail much longer than head and body'' (p. 407).

Each of the three species was represented by only the holotype. All three specimens have thick and soft fur (silky to the touch) and noticeably long facial vibrissae. All three holotypes are nearly indistinguishable in fur coloration: upperparts are dark brown with rich chestnut highlights and underparts are grayish white. Allen had noted the close similarity in color between *bolivaris* and *rivularis* and even used similar wording to describe chromatic characterizations of *bolivaris* and *castaneus*—the descriptions are essentially interchangeable between the two. The three specimens differ in tail lengths, which Allen noted, but that disparity partly reflects preparation technique. The holotype of *boliviaris* has the tail shoved into the body; prepared normally, the tail would be as long as that of *rivularis*. Other than this artifact, the three skins are so similar in body size and pelage color, at least to us, that they could have been part of one litter and are certainly representatives of a single species.

The chromatic contrast between *bolivaris* and members of the ''*O. magdalenae* group,'' which Allen mentioned, parallels the distinction between dark examples of *O. bolivaris* and specimens of *O. talamancae*, as we note elsewhere. Characteristics of vibrissae, body size, and fur texture and color in the three holotypes of Allen's species closely resemble these traits in the holotypes of *bombycinus* and *orinus*, both of which are of comparable age (table 48).

Values for cranial measurements of Allen's holotypes are also similar to those obtained from holotypes of *bombycinus* and *orinus*; and values for molar measurements from all holotypes, including *alleni* (which is the only very young adult), are not very different (table 48). The close correspondence in cranial and dental values among Allen's three holotypes can also be appreciated by visual inspection of the crania; the three skulls are much alike in overall size and conformation (figs. 126–128). Finally, in all six holotypes, the parietal–squamosal suture is confined to the temporal ridge and the parietal does not extend ventrally to form part of the lateral braincase wall (table 31; also shown in fig. 128), a diagnostic trait shared by nearly all examples of the species Pine (1971) reviewed as *O. bombycinus*, which should now bear the name *O. bolivaris*.

ORYZOMYS TALAMANCAE

Oryzomys talamancae Allen (1891: 193). TYPE LOCALITY: Costa Rica, Provincia de Limón, Talamanca (locality 3 in gazetteer and fig. 66). HOLOTYPE: USNM 12222/22742 (skin and skull; figs. 129, 130), an adult male from the W. M. Gabb collection.

Oryzomys mollipilosus Allen (1899: 208). TYPE LOCALITY: Colombia, Departamento de Magdalena, Valparaíso, 4500 ft (= Cincinati, locality 56 in gazetteer and fig. 66). HOLOTYPE:

AMNH 15323 (skin and skull), an adult female collected May 10, 1899 by H. H. Smith.

Oryzomys magdalenae Allen (1899: 209). TYPE LOCALITY: Colombia, Departamento de Magdalena, Minca, 2000 ft (locality 55 in gazetteer and fig. 66). HOLOTYPE: AMNH 15318 (skin and skull), an adult female collected August 3, 1899 by H. H. Smith.

Oryzomys villosus Allen (1899: 210). TYPE LOCALITY: Colombia, Departamento de Magdalena, Valparaíso, 4500 ft (= Cincinati, locality 56 in gazetteer and fig. 66). HOLOTYPE: AMNH 15321 (skin only), an adult female collected April 15, 1899 by H. H. Smith.

Oryzomys sylvaticus Thomas (1900: 272). TYPE LOCALITY: Ecuador, Provincia del Oro, Santa Rosa, 10 m (locality 98 in gazetteer and fig. 66). HOLOTYPE: BMNH 0.1.1.21 (skin and skull), an adult male collected June 30, 1899 by P. O. Simons.

Oryzomys panamensis Thomas (1901a: 252). TYPE LOCALITY: Panamá, Provincia de Panamá, City of Panamá (locality 15 in gazetteer and fig. 66). HOLOTYPE: BMNH 0.5.1.67 (skin and skull), an old adult female collected February 25, 1899 by E. Andre.

Oryzomys medius Robinson and Lyon (1901: 142). TYPE LOCALITY: Venezuela, Distrito Federal, San Julián, 8 miles E La Guaira (locality 80 in gazetteer and fig. 66). HOLOTYPE: USNM 105405 (skin and skull), a young adult male collected August 8, 1900 by W. Robinson.

Oryzomys carrikeri Allen (1908: 656). TYPE LOCALITY: Costa Rica, Provincia de Limón, Río Sicsola, Talamanca (locality 3 in gazetteer and fig. 66). HOLOTYPE: AMNH 25976 (skin and skull), an adult female collected August 18, 1904 by M. A. Carriker, Jr.

Fig. 129. Dorsal, ventral, and lateral views of the cranium from holotype of *Oryzomys talamancae* Allen (USNM 12222/22742), an adult male from ''Talamanca,'' Costa Rica. ×2. Measurements (in mm) are: ONL = 31.4, ZB = 15.4, IB = 5.1, LR = 10.4, BR = 5.9, HBC = 8.5, BZP = 2.6, LD = 8.1, LBP = 7.8, PPL = 10.2, LIF = 4.5, BIF = 2.3, CLM1–3 = 4.4, BM1 = 1.2.

EMENDED DIAGNOSIS: An oryzomyine of moderate body size with tail longer than length of head and body; fur over dorsum bright tawny or tawny brown with ochraceous tones along sides of head and body, underparts grayish white; tail bicolored, mottled ventrally toward tip; dorsal surfaces of front and hind feet densely covered by white hairs, claws concealed by long and thick sheaths of ungual tufts; superciliary, genal, and mystacial vibrissae moderately long, extending only to ears but not beyond; cranium elongate, dorsolateral margins of interorbit ridged, parietal contributes to side of braincase in form of winglike extension ventral to temporal ridge; moderately long and narrow incisive foramina; no alisphenoid struts; complete cephalic arterial pattern marked by sphenofrontal foramen, squamosoalisphenoid groove, large stapedial foramen, and prominent groove on ventral surface of pterygoid plate for infraorbital branch of stapedial artery; ascending ramus of dentary low (dentary appears elongate compared with *O. bolivaris*); second upper molar with long paraflexus and labial fossette only, medial fossette absent; second lower molar with deep hypoflexid extending most of way across tooth, shallow entoflexid, and no fossettid; chromosomes 2*n* = 34 or 40–42 and FN = 63–67 representing two obviously separate populations in Venezuela, 2*n* = 36 or 54 and FN = 60 representing two populations, one north and the other south of the Golfo de Guayaquil, Ecuador.

DISTRIBUTION: Evergreen and deciduous

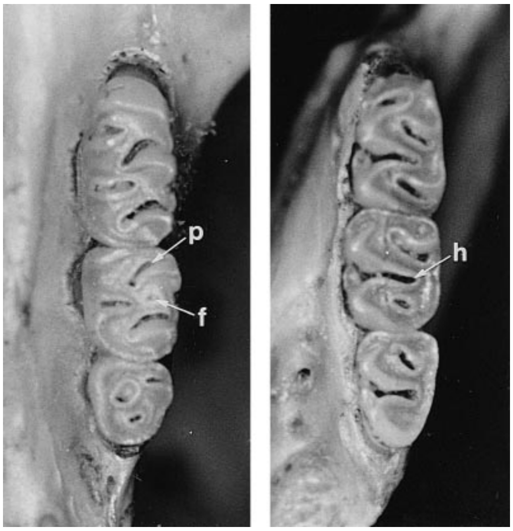

Fig. 130. Occlusal views of left upper (CLM1–3 = 4.4 mm) and lower molar rows of the holotype of *Oryzomys talamancae* (USNM 12222/22742). The second upper molar (**left view**) has a long paraflexus (**p**) and labial fossette (**f**). In the second lower molar (**right view**), the long hypoflexid (**h**) nearly bisects the tooth. See discussion in text.

tropical forests in the trans-Andean region from northwestern Costa Rica, east through Panamá into Colombia west of the Cordillera Occidental, northwestern Venezuela, and west of the Andes in Ecuador; documented elevational range extends from near sea level to about 1524 m.

REMARKS: Exact location of the type locality for *talamancae* is ambiguous. ‘‘Talamanca’’ may refer to a village (09°36′N/82°47′W; USBGN Costa Rica, 1983: 118), to the eastern lowlands adjacent to the Cordillera Talamanca (‘‘lowland areas up to 500 m in SE Limón,’’ McPherson, 1985: 269), or to the Cordillera Talamanca. W. M. Gabb, collector of the USNM specimens listed below, traveled throughout the Talamancan region and skin tags on his specimens are simply labeled ‘‘Talamanca’’; whether that refers to village, eastern lowlands, or cordillera is not known. Goldman (1918: 73) claimed that Talamanca was ‘‘probably near Sipurio [09°32′N/82°55′W, USGBN Costa Rica, 1983: 115] in the valley of the Río Sicsola [also spelled Sixaola].’’ The AMNH specimens listed in the gazetteer under Talamanca (locality 3) were collected by M. A. Carriker and skin labels on all of them bear the notation, ‘‘Río Sicsola, Talamanca.’’

Except for *sylvaticus*, reasons for associating the other scientific names we list as synonyms of *O. talamancae* have been documented elsewhere. Goldman (1918: 73) had already correctly placed the names *panamensis* and *carrikeri* as synonyms of *O. talamancae*, and Musser and Williams (1985) added *mollipilosus*, *magdalenae*, *villosus*, and *medius*. In addition to those, Musser and Williams listed *sylvaticus* and *castaneus* as synonyms, even though they had not examined the holotypes. However, *castaneus* belongs in the synonymy of *O. bolivaris*, an association we have already documented in the account of that species.

‘‘*Oryzomys sylvaticus*’’ was described by Thomas in 1900 (pp. 272–273):

> General appearance very much that of a large specimen of the European *Mus sylvaticus*. Fur straight, close and rather crisp, about 8–9 millim. long on the back. General colour above dull fulvous, much darkened with black on the middle line of the back, clearer on the sides. Head decidedly greyer than body. Under surface soiled whitish, the bases of the hairs slaty, the tips dull white; line of demarcation on sides rather sharply defined. Ears large, finely haired, dull brown. Outer sides of limbs greyish, inner sides like belly; hands and feet dull white above, wrists and ankles browner; feet long and slender, fifth hind toe reaching to the middle of the basal phalanx of the fourth. Tail slender, naked, finely scaled, brown above, scarcely paler below.
>
> Skull very similar in its general shape and delicate build to that of *O. gracilis*, but much larger. Nasals and premaxillae about level posteriorly. Supraorbital edges evenly divergent, finely beaded, the beading extending backward nearly half across the parietals. Palatal foramina small and narrow. Teeth of normal proportions.

‘‘This species,’’ continued Thomas, ‘‘is exactly intermediate in size between the large *O. laticeps* and the small *O. gracilis*, and may therefore be readily distinguished by size from either of them, to which alone it has any resemblance in general characters. Probably it is most nearly allied to *O. gracilis*.’’

The species Thomas knew as *O. laticeps* and *O. gracilis* are the same ones we refer to as *O. megacephalus* and *O. alfaroi*, respectively. Thomas’s values for greatest length of skull and length of molar row for *sylvaticus*, like our samples of *O. talaman-*

Fig. 131. Dorsal, ventral, and lateral views of crania from holotypes representing *Oryzomys nitidus*. Left trio portrays lectotype of *O. nitidus* Thomas (BMNH 85.4.1.41), a young adult male from Amable María, Perú. Right trio is holotype of *O. boliviae* Thomas (BMNH 1.1.1.64), an adult male from Mapiri, Bolivia. ×2. Measurements are listed in table 49.

cae, are smaller than those measurements of *O. megacephalus* from populations along the eastern foothills of the Ecuadoran Andes (table 35), but larger than our sample of *O. alfaroi* from Ecuador (table 34). Qualitative traits exhibited by the holotype of *sylvaticus* (derived from observations made independently by A. L. Gardner in the late 1970s and G. G. Musser in the early 1990s at the British Museum) match specimens of *O. talamancae* from Santa Rosa in the American Museum that were obtained by G.H.H. Tate in the 1920s (see locality 98 in gazetteer for *O. talamancae*). All share a bright and tawny brown dorsal coat (shorter and brighter than is typical of *O. bolivaris*), superciliary and genal vibrissae that reach only the ears when laid against side of the head (not extending far beyond as in *O. bolivaris*), similar cranial conformation, and a prominent winglike extension of the parietal ventral to the temporal ridge (common to *O. talamancae*, but undiagnostic of *O. bolivaris* in which the parietal does not form part of the braincase wall below the temporal ridge). The holotype of *sylvaticus* is a clear example of *O. talamancae* and not *O. bolivaris*.

ORYZOMYS NITIDUS

Hesperomys laticeps var. *nitidus* Thomas (1884: 452). TYPE LOCALITY: Perú, Departamento de Junín, Amable María (locality 63 in gazetteer and fig. 79). LECTOTYPE (designated by Thomas, 1927b: 549): BMNH 85.4.1.41 (body in fluid and skull, fig. 131; measurements listed in table 49), a young adult male collected by C. Jelski.

Oryzomys boliviae Thomas (1901c: 536). TYPE LOCALITY: Bolivia, Departamento de La Paz, Mapiri, 800 m (locality 80 in gazetteer and fig.

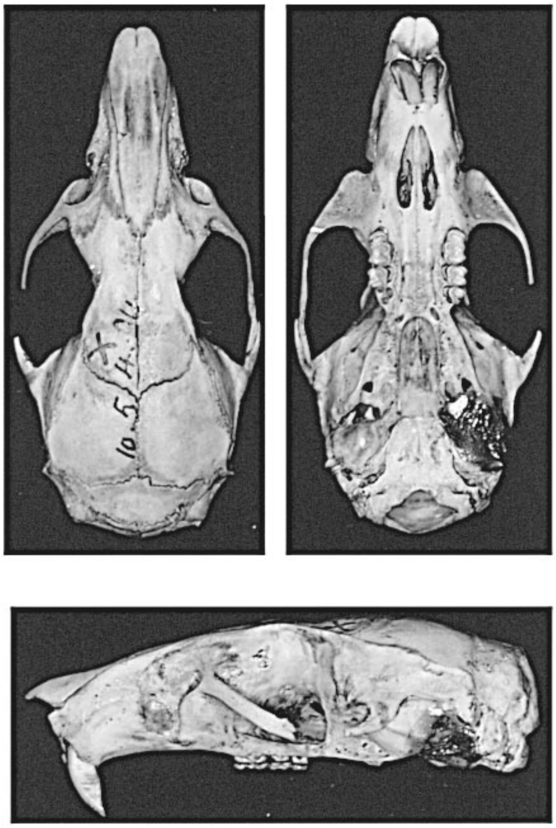

Fig. 132. Dorsal, ventral, and lateral views of the cranium from holotype of *Oryzomys macconnelli* Thomas (BMNH 10.5.4.34), an old adult female from Supenaam River, Guyana. ×2. Measurements are listed in table 49.

79). HOLOTYPE: BMNH 1.1.1.64 (skin and skull, fig. 131; measurements listed in table 49), an adult male collected August 29, 1900 by P. O. Simons.

EMENDED DIAGNOSIS: An oryzomyine of medium body size with tail about as long as length of head and body (shorter or longer in different geographic samples); upperparts bright tawny or tawny brown with ochraceous highlights along sides of head and body, whitish gray ventral pelage; tail monocolored, mottled on ventral surface near tip; dorsal surfaces of front and hind feet covered with dense white hairs, claws nearly hidden by long and dense ungual tufts, all plantar pads present; superciliary, genal, and mystacial vibrissae moderately long, not reaching beyond ear; cranium elongate, narrow interorbit (compared with *O. macconnelli*) bounded by dorsolateral ridges; alisphenoid struts present in about half of specimens examined; long and narrow incisive foramina, short bony palate, wide zygomatic plate with correspondingly deep zygomatic notch; complete cephalic arterial pattern, indicated by sphenofrontal foramen and squamosoalisphenoid groove, large stapedial foramen, and prominent trough on ventral surface of pterygoid plate for infraorbital branch of stapedial artery; prominent coronoid process on dentary (compared with *O. macconnelli*); second upper molars with short paraflexus and labial as well as medial fossettes; second lower molar with moderately deep entoflexid and short hypoflexid extending only halfway across tooth, fossettid present; chromosomes $2n = 80$ and $FN = 86$.

DISTRIBUTION: Perú and Bolivia, western and south-central Brazil, eastern Paraguay, and northeastern Argentina; elevational range extends from about 50 to 1524 m.

REMARKS: Only one other scientific name, *boliviae*, can be associated with *O. nitidus* as a synonym. Thomas (1901c: 536–537) considered his new species, *Oryzomys boliviae*, to be a ‘‘Bolivian representative of *O. intermedius*; tail shorter and molars smaller,’’ and described it as follows:

> Size and general proportions as in the allied species. General colour above heavily lined fulvous brown, clearing into rich fulvous on the sides. Under surface dull white, fairly well defined; the bases of the hairs slaty.
>
> Head greyer and duller above, but cheeks like sides. Ears large, well-haired, wholly dark brown, darker than the head. Outer side of limbs fulvous to wrist and ankles, inner sides white; hands white, feet buffy white. Tail not or scarcely longer than the head and body, very finely haired and scaled, dull whitish below proximally, the upperside and end brown.
>
> Skull very similar to that of *O. intermedius*, with the same narrow muzzle, narrow interorbital region, well-developed zygomatic plate, and medium-sized palatal foramina. But the molars are markedly smaller in all the specimens examined.

Thomas ended the account of his new species with this statement of affinities: ‘‘In spite of the wide difference in locality between the habitats of *O. boliviae* and *intermedius* their resemblance to each other, both external and cranial, is so great that it is practically impossible to distinguish them except

TABLE 49
Measurements (mm), Age, and Sex of Type Specimens Identified as Examples of the *Oryzomys nitidus* Group

	O. macconnelli		*O. nitidus*		*O. russatus*		
	macconnelli[a]	*mureliae*[a]	*nitidus*[b]	*boliviae*[a]	*russatus*[b]		*intermedia*[b]
	BMNH	AMNH	BMNH	BMNH	NMW	NMW	UZM
	10.5.4.34	33756	85.4.1.41	1.1.1.64	B478	B481	7498
Age	Old adult	Adult	Young adult	Adult	Adult	Adult	Adult
Sex	Female	Male	Male	Male	Male	Male	Male
LHB	145	120	—	148	168[e]	150[e]	—
LT	159	150	—	150	145[e]	135[e]	—
LHF[d]	35	34	32	35	35	35	—
LE	24	—	—	25	20[e]	20[e]	—
ONL	35.5	—	—	34.5	36.3	35.7	35.1
ZB	17.0	—	15.8	17.6	18.2	17.7	17.7
IB	5.5	—	5.1	5.3	5.4	5.1	5.7
LR	11.7	—	10.4	11.3	11.8	11.7	11.4
BR	6.8	—	5.8	6.4	6.8	6.9	6.7
LB	13.3	—	—	13.3	13.1	12.6	13.1
HBC	9.3	—	—	8.7	—	9.2	9.2
BZP	3.9	—	3.7	4.2	4.4	4.0	3.9
LD	9.3	—	8.3	9.2	9.5	8.9	8.6
LBP	7.4	—	—	6.7	6.9	6.3	6.6
PPL	11.9	—	—	12.2	—	13.2	12.1
LIF	6.0	—	4.6	6.2	6.3	6.3	5.9
BIF	2.9	—	2.3	2.7	2.3	2.2	2.1
CLM1–3	5.1	—	4.8	4.7	5.1	5.0	4.8
BM1	1.4	—	1.4	1.4	1.5	1.6	1.4

[a] Holotype.
[b] Lectotype (B478) and syntype (B481).
[c] Paratype.
[d] Measured by G. G. Musser, unless otherwise indicated.
[e] Measured by Musser on the dry skin; measurement of ear is likely inaccurate because of its dry, distorted shape.

by the shorter tail and smaller molars of the new form."

Our analyses (fig. 114) indicate the holotype of *boliviae* to represent a sample of *O. nitidus*.

ORYZOMYS MACCONNELLI

Oryzomys macconnelli Thomas (1910: 186). TYPE LOCALITY: Guyana, District Demerara, along the Supenaam River (locality 9 in gazetteer and map in fig. 78). HOLOTYPE: BMNH 10.5.4.34, an old adult female (skin and skull, fig. 132; measurements listed in table 49) donated to the British Museum by F. V. McConnell.

Oryzomys incertus Allen (1913: 598). TYPE LOCALITY: Colombia, Departamento de Caquetá, Río Bodoquera, La Murelia, 600 ft (locality 16 in gazetteer and fig. 78). HOLOTYPE: AMNH 33756, an adult male (skin only; measurements listed in table 49) collected July 19, 1912 by L. E. Miller.

Oryzomys mureliae Allen (1915: 630). A replacement name for *Oryzomys incertus* Allen (1913), which is preoccupied by *Oryzomys alfaroi incertus* (see Allen, 1915).

EMENDED DIAGNOSIS: A medium-sized oryzomyine, with a tail equal to or longer than head and body, that closely resembles *O. nitidus*, differing by having lax and long pelage in most samples, narrower zygomatic plate with correspondingly shallower zygomatic notch, wider interorbit, shorter and wider incisive foramina, longer bony palate, and alisphenoid struts absent from 99% of specimens examined; chromosomes $2n = 64$ and $FN = 64$ or 70 (Perú and Brazil, respectively); $2n = 76$ and $FN = 85$ (Venezuela).

DISTRIBUTION: Tropical evergreen rain for-

TABLE 49
(Continued)

	O. russatus						*O. emmonsae*
	coronatus[a] UZM —	*lamia*[a] BMNH 1.11.3.32	*legatus*[a] BMNH 25.2.1.24	*kelloggi*[c] AMNH 203073	*moojeni*[c] AMNH 203074	*physodes*[a] ZMB 1683	*emmonsae*[a] MZUSP 27150[g]
Age	Adult	Adult	Adult	Adult	Young adult	Adult	Old adult
Sex	?	Male	Male	Male	Male	Male (?)	Male
LHB	—	145	140	170	140	ca. 150[f]	142
LT	—	153	164	150	130	ca. 165[f]	160
LHF[d]	—	36	35	35	35	ca. 36[f]	34
LE	—	24	25	—	—	?	24
ONL	—	35.9	36.2	35.3	34.1	—	34.4
ZB	—	19.0	18.2	19.1	17.1	—	176
IB	5.5	5.9	5.8	5.5	5.5	ca. 5.6	5.4
LR	—	12.1	12.9	11.6	11.3	—	12.2
BR	—	7.3	6.8	7.5	6.1	ca. 6.2	6.9
LB	—	13.4	13.0	13.6	13.0	—	12.3
HBC	—	9.5	8.7	9.8	9.2	—	9.7
BZP	4.2	4.8	4.7	3.8	3.5	4.1	4.1
LD	8.9	9.6	9.3	8.6	8.5	—	9.3
LBP	—	7.9	7.2	6.6	6.3	6.4	6.7
PPL	—	12.1	12.4	12.8	11.7	—	11.3
LIF	6.2	6.0	5.5	6.0	6.0	?	5.3
BIF	2.6	2.3	2.3	2.2	2.3	?	2.4
CLM1–3	5.4	5.3	5.1	5.1	5.4	4.9	4.8
BM1	1.5	1.5	1.4	1.6	1.5	1.4	1.4

[f] Measured by R. S. Voss on the dry skin. Approximately 165 mm is the length obtained from converting the measurements for the holotype given by Burmeister (1854: 167), which is within the range of variation we recorded for samples of *O. russatus* (table 37). Thomas studied the holotype of *physodes* and recorded lengths of head and body, tail, and hind foot as 155 mm, 163 mm, and 33.6 mm, respectively (Thomas's notebook made during his visits to European museums, in archives of British Museum).

[g] Body measured after capture by L. H. Emmons; external measurements are taken from label attached to skin. Cranium and dentition were measured by M. D. Carleton.

ests of Amazonia; documented elevational records extend from near sea level to 1524 m.

REMARKS: Only two other scientific names can be tied to *O. macconnelli*. The holotype of *Oryzomys incertus* (AMNH 33756) was collected by L. E. Miller at La Murelia (locality 16 in gazetteer), Colombia. Allen's (1913: 598–599) description was based on the stuffed skin, the only component of the type that exists:

> Upperparts deep ochraceous orange, varied strongly with black throughout the dorsal region; flanks deep orange, forming a broad lateral line sharply defined against the ventral surface, which is clear white superficially with the basal third of the pelage deep plumbeous; top and front of the head like the back, not *darker* nor *grayer*; ears large, nearly naked, dark brown, in strong contrast with the surrounding pelage; feet light yellowish brown; tail light brown, indistinctly bicolor on the basal third.

The specimen so impressed Allen that he remarked:

> The affinities of this species appear to be with the *O. subflavus* group, particularly with *O. lamia* Thomas of southwestern Minas Geraes, but on geographical considerations it is not likely to prove the same. It is wholly unlike any of the described species from Colombia. On comparing recently the type specimen with the material in the British Museum I was unable to find any species to which it could be referred.

Two years later, Allen (1915) had to correct himself: "I am indebted to Mr. E. A. Goldman for kindly calling my attention to the preoccupation of the name *Oryzomys incertus* . . . by my previous *Oryzomys alfaroi incertus*. . . . My later *O. incertus* is here renamed *Oryzomys mureliae*, after the type locality.''

Tate (1939) recognized the holotype of *mureliae* to be an example of *O. macconnelli*; it has the characteristic pelage traits of that species (long and lax fur that is bright tawny brown).

ORYZOMYS EMMONSAE

Oryzomys emmonsae Musser, Carleton, Brothers, and Gardner (present report). TYPE LOCALITY: Brazil, Estado de Pará, E bank Rio Xingu, 52 km SSW Altamira (locality 148 in gazetteer and fig. 79). HOLOTYPE: MZUSP 27150 (skin, skull, karyotype, biopsy tissues, figs. 107–109; measurements listed in table 49), an old adult male collected September 3, 1986 by L. H. Emmons.

DIAGNOSIS: Superficially similar to *Oryzomys nitidus*, but with a relatively longer tail, smaller and more gracile cranium, and different cranial proportions; chromosomes $2n = 80$ and $FN = 86$.

DISTRIBUTION: Amazonia south of the Rio Amazonas between the lower portions of the Xingu and Tocantins rivers.

ORYZOMYS RUSSATUS

Mus physodes Brants (1827: 139). TYPE LOCALITY: Brazil, ''Provinz San Paulo'' [= Estado do São Paulo] (Lichtenstein, 1830: text for plate 34, fig. 1). HOLOTYPE: ZMB 1683 (skin and skull, fig. 134; measurements listed in table 49), an adult male collected by Beske. Preoccupied by *Mus physodes* Olfers (1818).

Hesperomys russatus Wagner (1848: 312). TYPE LOCALITY: Brazil, Estado do São Paulo, Ipanema (locality 182 in gazetteer and fig. 79). LECTOTYPE: NMW B478 (skin and skull, figs. 135, 136; measurements listed in table 49), an adult male collected May 25, 1822 by J. Natterer.

Hesperomys laticeps var. *intermedia* Leche (1886: 693). TYPE LOCALITY: Brazil, Estado do Rio Grande do Sul, Taquara do Mundo Novo (locality 171 in gazetteer and fig. 79). LECTOTYPE: UZM 7498 (skull only, fig. 138; measurements listed in table 49), an adult male collected by Bischoff.

Calomys coronatus Winge (1887: 51). TYPE LOCALITY: Brazil, Estado de Minas Gerais, Lagoa Santa (locality 198 in gazetteer and fig. 79). HOLOTYPE: Uncataloged partial cranium (fig. 139; measurements listed in table 49) from Lapa da Serra das Abelhas in paleontological collections of UZM, collected by P. W. Lund.

Oryzomys lamia Thomas (1901b: 528). TYPE LOCALITY: Brazil, Estado de Minas Gerais, Río Jordão near Araguary, 900 m (locality 199 in gazetteer and fig. 79). HOLOTYPE: BMNH 1.11.3.32 (skin and skull, figs. 140, 141; measurements listed in table 49), an adult male collected July 10, 1901 by A. Robert.

Oryzomys legatus Thomas (1925: 577). TYPE LOCALITY: Bolivia, Departamento de Tarija, Caraparí, 1000 m (locality 158 in gazetteer and fig. 79). HOLOTYPE: BMNH 25.2.1.24 (skin and skull, figs. 140, 141; measurements listed in table 49), an adult male collected August 6, 1924 by E. Budin.

Oryzomys kelloggi Ávila-Pires (1959a: 2). TYPE LOCALITY: Brazil, Estado de Minas Gerais, Fazenda São Geraldo, Além Paraíba, 140 m (locality 195 in gazetteer and fig. 79). HOLOTYPE: NM 7335 (skin and skull), an adult male collected May 21, 1943.

Oryzomys ratticeps moojeni Ávila-Pires (1959b: 3). TYPE LOCALITY: Brazil, Estado do São Paulo, Morro de São João, Cananéia, 6 m (locality 174 in gazetteer and fig. 79). HOLOTYPE: MN 22.908 (skin and skull), an adult male collected August 23, 1956.

EMENDED DIAGNOSIS: An oryzomyine of large body size with a tail equal to or longer than head and body, and closely similar to *O. nitidus* in all traits, differing by its generally brighter dorsal pelage, by greater external, cranial, and dental dimensions on average, and by the usually shorter incisive foramina relative to occipitonasal length in most; chromosomes $2n = 80$ and $FN = 86$.

DISTRIBUTION: Rainforest habitats along Andean foothills in southern Bolivia and northern Argentina, riverine rain forests in south-central Brazil, and tropical and subtropical evergreen rain forests in southeastern Brazil. Known elevational range extends from near sea level to 2100 m.

The use of *russatus* as the oldest name for the species, and reasons for associating the synonyms listed with it are documented below.

ALLOCATION OF *PHYSODES*: This animal was described by Brants in 1827 (p. 139), although the name is often attributed to Lichtenstein, as Brants himself did. A translation from the Dutch follows (made by E. Brothers; the Dutch version is reproduced in appendix N):

53. (26) M. PHYSODES Lichtenstein. The three-fingered rat.

Beautiful red-brown on the back, pure white on the underside, both colors sharply separated, only three conspicuous fingers on the forefeet.

Measurements:

Length from nose to tail	6	duim	8	lyn
Length of tail	5	—	9	—
Length of head	1	—	5	—
Length of ear	-	—	6	—
Length of hind foot	1	—	4	—

The color over the entire upper side of the body and head is a rather uniform reddish brown mixed with many longer black guard hairs, especially along the middle of the back; also notable is the pure white color of the underside, the insides of the limbs, the feet and hands, and the bottom half of the upper lip almost as far as the eyes. The transition from the russet of the dorsum to the white underneath is a rapid one. The hair itself is very soft, glossy, and close-lying, slate-colored at its origin. The body is elongate with a moderately pointed head; the ears are white of color, hairless and very large, the ear opening is clearly visible, the snout bears a strongly projecting hair crest, the upper lip is split and the incisors are colored. Scaly skin covers the feet. The front feet have only three obvious fingers; the stump-like thumb is placed very high on the foot and bears a weakly formed nail. The small finger, similarly not much more than an almost imperceptible stump, bears however a small, well-formed nail. The hind feet have five fingers and, just like those of the fore feet, have curved white claws and a covering of long white hair. Of moderate length, the tail is white and nearly hairless. Overall, the body is very elongate and not inelegant; its native land is Brazil.

Specimens are housed in the museums of Berlin, Brazil, and Vienna.[9]

The same taxon was described by Lichtenstein (1830) in text and with a color plate (see fig. 133 where the plate is reproduced accompanied by an English translation of the description in the legend). In 1854, Burmeister (p. 167) redescribed *physodes* as a species of *Hesperomys* in a subsection of that genus labeled *Holochilus*, and also allied Wagner's *russatus* with it (translation by E. Brothers; see appendix P for the original German version):

4. Hesperomys physodes *Licht*.

Wagn. Schreb. Suppl. III. 535. 26.

Mus physodes *Brants* Muiz. 139. 53. -– *Lichtenst*. Darst. n. Säugeth. etc. Taf. 34, Fig. 1.

? Hesper. russatus *Wagn*. Münch. Acad. Abh. V. 312. 6.

Light cinnamon-brown on the dorsum, pure white on the belly, the two colors set against each other sharply; the naked tail is somewhat shorter than the body; the body is 6⅔″, the tail is 6⅓″.

Very dainty and fine of build, especially the feet and tail, but the ears are large.—The pelage is smooth, short, and clings tightly to the body, but is soft to the touch. The entire dorsum from the snout to the tail is light red-yellow-brown, a touch of cinnamon with orange; the cheeks are the same, but the upper lip and the neck behind the cheeks are white; the legs are completely cinnamon red on the outside, and white on the inside; the feet and toes are also white; the white areas are always sharply delineated from the cinnamon-red parts. Each hair is a handsome lead gray near the base and cinnamon-red or white at the end; some of the dorsal hairs have darker, brown tips; these are very fine, and short; a few of the remaining hairs are distinctly akin to whiskers. The dorsal coat has a crest. The rounded ears are large, wide and vaulted, naked inside, with hair around the perimeter, especially the outside edge. The color is red-brown, with a patch of whiter hair from the tip to the back side. Whiskers fine and brown, the lower ones white. Feet are dainty, the front ones slender because the thumb is very small, though not entirely lacking; the outer toe is likewise very small but present; the three middle toes are very unequal, the center toe is strong and the outer ones greatly shortened. The hind feet are somewhat less constricted, with the toes bare and relatively long; the three middle toes are almost of equal length, the centermost extending just a little farther. Soles are naked, flesh-colored, textured like inferior shagreen [*translator's note* – shagreen is ‘‘a kind of untanned leather prepared in Russia and the East, from the skins of horses, asses, camels, etc., and covered with small round granulations by pressing small seeds into the grain or hair side when moist, and when dry scraping off the roughness. Soaking then causes the compressed or indented portions to swell up into relief’’; Webster's 2nd New International Dictionary (1961: 2299)], the undersides of the toes are nearly smooth. The tail is very gracile, extremely scaly, sparsely haired, and weakly colored. -– Total length 13″, body 6″8‴, head to ear 1″5‴, tail 6″4‴, ear 7‴, hind foot 1″4‴. -— São Paulo.[9]

Note. I have sent my precise description of the original specimen to Berlin; G. R. Lichtenstein and Brants, to a greater degree, give the tail as too short, while the hairy ½″ stretch near where it separates from the body mass is incorrect. The species is allied primarily with Hol[ochilus] leucogaster *Brandt* and to Hesp[eromys] russatus *Wagn*. (loc. cit.). The yellowish trace on the belly and the lively color of the back are prominent distinctions of the latter.

Since the time when Burmeister was writing, *physodes* has been associated with *Holochilus*, either as a species (Fitzinger, 1867: 90; Trouessart, 1898: 521, 1904: 411; Gyldenstolpe, 1932: 63; Ellerman, 1941: 462) or placed in the synonymy of *Holochilus brasiliensis* (Hershkovitz, 1955: 665; Cabrera, 1961: 505).

The holotype of *Mus physodes* Brants was studied by A. L. Gardner in 1978 and by R. S. Voss in 1996 during visits to Berlin. The following description is abstracted and syn-

Fig. 133. Reproduction of Lichtenstein's (1930) color plate of *Mus physodes* Brants (reduced from the original). A translation of the German text (by E. Brothers; the original German version is reproduced in appendix O) that accompanies the plate is as follows:

34th Plate
1st Figure
MUS PHYSODES Lichtenstein
The tridactylous rat.

Species Description: As big as a young house rat, with long hind feet, long tail, large naked ears, only three obvious toes on the front feet; body is yellow-brown above, pure white below.

Measurements:[9]

Greatest length from snout to base of tail	7 Zoll	0 Linie
Length of tail	6 Zoll	0 Linie
Length of head, to the nape of neck	2 Zoll	0 Linie
Length of ear	0 Zoll	7 Linie
Breadth of ear	0 Zoll	6 Linie
Length of hind foot, from heel to claw tip	1 Zoll	5 Linie

The hair is quite stiff and dense, light gray near the skin, yellow-brown at the outer margin, brown-tipped on the dorsum. On the flanks, the red-brown color is sharply divided from the pure white of the venter in a straight line from the knee to the elbow. The four feet, as well as the entire underside of the naked tail, are also white. The outer toe of the forefoot is a short little stump with a small rounded nail. As for the three remaining toes, both outer toes are of nearly equal length, while the inner one is considerably shorter. The hair crest is high and the beard bristles [mystacial vibrissae] are longer than the head, very fine and of a browner color.

This species is closely related to Azara's *Anguya* . . ., deviating in the slightly livelier coloring, lack of enough correct measurements, and the unmentioned, at least by Azara, tridactyly. The habitat is the Brazilian province of São Paulo.

thesized from their notes. The specimen bears the number ZMB 1683, and the catalog contains the following information about it, written in W. Peters' hand: ''Hesperomys (Holochilomys) physodes Lichtenstein*/non Holochilus leucogaster Brants—Brasilien Beske [name of the collector].'' No sex is indicated on any tags or in the catalog. Gardner could not find mammae on the skin and regarded the animal as a male. Dorsal pelage over head and body is bright tawny, including the ears, and only slightly paler on the

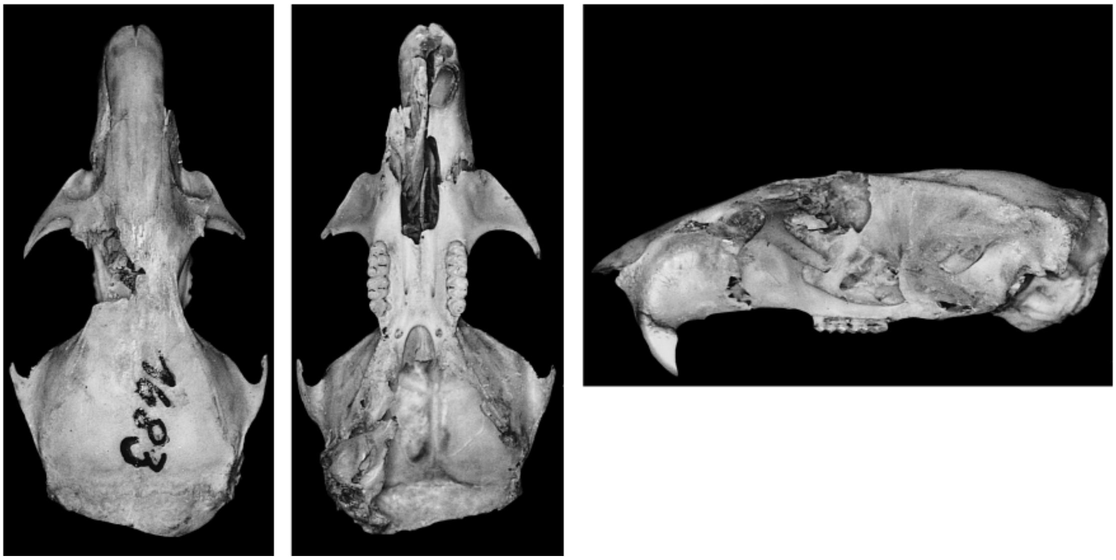

Fig. 134. Dorsal, ventral, and lateral views of the cranium from the holotype of *Mus physodes* Brants (ZMB 1683), an adult male from ''Provinz San Paulo,'' Brazil. ×2. Measurements are listed in table 49.

sides. Underparts are white (with some gray of the hair bases showing through) and contrast sharply with the dorsum; the white extends to beneath the nose and eyes. The tail is longer than head and body and bicolored for much of its length, brown above and pale below. Dorsal surfaces of hind feet are white with thick tufts of long hairs extending beyond and concealing the claws.

The skull is incomplete (fig. 134). Occipital region, left bulla, right premaxillary and incisor are missing. The zygomatic arches are broken. Molar-bearing portions of each dentary with an intact coronoid process on the left one are all that remain of the mandible. Incisive foramina are long and narrow, their posterior margins situated anterior to the alveoli of the first upper molars. The cephalic arterial circulation is primitive as indicated by an squamosoalisphenoid groove (in which the supraorbital branch of the stapedial artery courses). Each second upper molar has a weak medial fossette.

The holotype of *physodes* is not an example of *Holochilus*. It does not possess any of the distinctive characteristics of that genus, such as nearly naked claws, conspicuous natatory fringes and highly developed interdigital webbing on the hind feet, and derived cephalic arterial pattern (Voss and Carleton, 1993). Traits of the holotype match those associated generally with species of Brazilian *Oryzomys* and particularly with *O. russatus* (formerly referred to as *O. intermedius*): bright tawny dorsum, white venter, white feet with claws concealed in long and thick ungual tufts, squamosoalisphenoid groove (a vascular groove indicating passage of the supraorbital branch of the stapedial; see Carleton and Musser, 1989), and medial fossette on second upper molar.

For more than a century, published synonymies have associated *physodes* with *Holochilus*, but no such attribution can be found in the publications of Oldfield Thomas. That astute mammalogist had settled the identity of *physodes* when he visited several European museums in the late 1800s and studied important types housed there. Thomas recorded his observations in a journal (the original is at the British Museum; a photographed copy made by G.H.H. Tate in 1937 is stored in Mammalogy Archives, AMNH) and published some of them (Thomas, 1901b: 528, for example, where he mentioned studying the holotype of *Hesperomys subflavus*). In most of his published reports, however, Thomas did not explicitly state that he had studied a certain type, but the results of his examinations were often reflected in his comparisons between new taxa he was describing and others previously described. For example, in Thomas's (1904: 142) description of *Oryzomys oniscus*, which was based on a sample collected by A. Robert from Estado do Pernambuco, Brazil, he compared the new species to ‘‘*O. physodes*, Licht. (Rio Janeiro and Espírito Santo), *O. lamia*, Thos. (Minas Geraes), and *O. intermedius*, Leche (São Paulo to Rio Grande do Sul), of all of which Mr. Robert has obtained specimens. . . .’’ Thomas had studied the holotype of *physodes* at Berlin and realized it was a species of *Oryzomys*, not *Holochilus* (an entire page of his journal is devoted to the type of *physodes*). Furthermore, his grouping of *physodes* with *lamia* and *intermedius*, all of which he noted had ‘‘rufous or buffy body-colour,’’ is a testament to his critical faculties and anticipated our union of the three by 95 years.

Although *physodes* (Brants, 1827) is the oldest name for the species we call *Oryzomys russatus*, it cannot be used because Olfers had already proposed *Mus physodes* in 1818. Olfers' (1818) name was associated with the genus *Reithrodon* (Hershkovitz, 1959) and is currently listed as a synonym of *R. auritus* (Musser and Carleton, 1993: 740).

IDENTIFICATION OF *RUSSATUS* AND SELECTION OF LECTOTYPE: Here we explain why the name *russatus*, traditionally associated with *Holochilus*, applies to a Brazilian species of *Oryzomys* related to *O. nitidus*. We begin by repeating a translation of Wagner's (1848: 312) description of *Hesperomys russatus*,[11] or ‘‘Die goldfalbige Scharrmaus’’ (the original in German is reproduced in appendix Q):

> The dorsum is vibrant golden pale orange flecked with a little black, somewhat lighter to the sides. The underside is sharply delineated and is a beautiful yellow-white, becoming paler at the neck and the medial surfaces of the hind legs. The feet have dirty white fur and the soles are bare. The ears have a hint of fine hairs; the tail is nearly hairless, pale, and darker on the dorsal surface.
>
> This Scharrmaus, brought back by Natterer from Ypanema, is so similar to *Mus physodes* Licht, that it is only by the vibrant coloration, the sparse yellow of the underside and snout-tip of the former, which is the only specimen known to exist in Berlin, that they appear to be distinguished. However, as they share the same home country, they might be considered merely as color variations of one and the same species.

Measurements Wagner provided are: body, 6″ 4‴ [6⅓ in.]; tail, 5″ 9‴ [5¾ in.]; ear, 0″ 7½‴ [⅔ in.]; hind foot, 1″ 5‴ [1½ in.].[9]

Apparently the description was based upon a single adult collected in 1822 by Johann Natterer from Ipanema, São Paulo, Brazil (locality 182 in gazetteer of *O. nitidus* group and account of *O. russatus*). Wagner (1848) did not identify the specimen he described by either collector or catalog number, and he did not designate a holotype.

Until now, Wagner's *russatus* has always been associated with *Holochilus* (Fitzinger, 1867: 90; Trouessart, 1898: 521, 1904: 411; Gyldenstolpe, 1932: 63; Ellerman, 1941: 462; Hershkovitz, 1955: 661, 666; Cabrera, 1961: 505; Musser and Carleton, 1993: 704), but Wagner's description does not apply to any example of *Holochilus* as we understand the morphological characteristics of species in that genus. Adults of *H. brasiliensis* (from Uruguay) and *H. sciureus* (from Goiás, Brazil) in the American Museum (the samples at hand that come from localities closest to Ipanema) have dark upperparts that are tawny or brown with a dark brown or blackish over-

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[11] Wagner (1848: 306) described *russatus* under a subheading (‘‘b, tawny pelage, tail equal to or shorter than body’’) of *Hesperomys* (‘‘Scharrmaus’’):

> This genus, of which until now only a few species could be counted in our collection from Brazil, is suddenly augmented by a considerable number of species brought back from this realm through Natterer's journey. In an earlier note of mine, a complete illumination of the genus *Mus* of the entire American continent was begun, to which important new information is now added. From all of those species which I have been able to examine, it is revealed that they belong not to *Mus* but to *Hesperomys*, or a closely related genus. Natterer did indeed collect quite a few specimens that have the tooth structure of *Mus*; these however are determined to be most likely derived from the Old World. Upset and interrupted by Natterer's recent and sudden death, I still must finish my examination of the tooth structure in all of the following listed species; however, I have no doubt that they will prove to be members of *Hesperomys*. Along with the Brazilian species I have also included one from Labrador, as proof that this genus occurs across the entire continent. (Translated from the German by E. Brothers.)

lay from head to rump. By contrast, the dorsum of *russatus* is ‘‘vibrant golden pale orange flecked with a little black.’’ Most of the *Holochilus* from Goiás have rich buffy or buffy orange venters; those from Uruguay are paler and some have white venters but even these express a buffy pectoral collar or streak; none are the ‘‘beautiful yellow-white’’ described for *russatus*. Ears of *Holochilus* are densely haired and unlike *russatus* in which the ears ‘‘have a hint of fine hairs.’’ Finally, adult examples of *Holochilus* are conspicuously larger than the animal Wagner described. Tails typically range from 6½ to 8 inches long (5¾ in *russatus*) and hind feet are 2 inches long (1½ in *russatus*). Natterer did collect examples of *Holochilus* at Ipanema, and Pelzeln (1883: 73) described these (one young female and three old males) under *Holochilus brasiliensis*. Highlights of his description include round rather than oval ears, long (about 2 inches) and partially webbed hind feet, digits with very short and silvery hairs, and long tails (8½–9½ inches); these are traits characteristic of *Holochilus*.

Within the sigmodontine fauna known from the region of Ipanema where Natterer worked (see Vanzolini, 1993, who reconstructed Natterer’s itineraries in Brazil), the species usually called *Oryzomys intermedius* (Musser and Carleton, 1993: 722) is the only one in which color of fur and magnitude of external dimensions correspond to Wagner’s description of the rat from Ipanema. Because *russatus* is an older name than *intermedius* and potentially applies to the same species, we were compelled to determine if one of Natterer’s specimens existed that could have been used by Wagner to describe *russatus*, thus allowing us to associate the name with a type specimen. Our quest involved correspondence with colleagues in Germany and Wien, searches through the older literature, and study of Natterer’s material at Wien, of which some specimens were loaned to us for reexamination. We were significantly aided by Barbara Herzig at Naturhistorisches Museum Wien, who loaned us specimens, searched through the old files made during Natterer’s time, answered our many questions (in letters on file in Mammalogy Archives, AMNH), and provided thoughtful suggestions.

Our first step was to contact Richard Kraft at the Zoologische Staatssammlung München and determine whether a holotype for Wagner’s *russatus* was stored there or whether they had any examples of *Oryzomys* and *Holochilus* collected by Natterer from Ipanema. Specimens were exchanged between Wien and München in the 19th century and types for some of the other taxa Wagner described are now housed at München. Kraft and Michael Hiermeier searched the collection and assured us that it did not contain either a type for *Hesperomys russatus* or any of Natterer’s material from Ipanema (personal commun.; letters from M. Hiermeier in Mammalogy Archives, AMNH).

We then turned to the volume written by Pelzeln (1883) that ‘‘brought together most, if not all, available taxonomic descriptive, and geographic data’’ (Hershkovitz, 1987: 38) associated with the mammals Natterer had collected during his expedition to Brazil. Pelzeln referred specimens, identified by Natterer’s collecting numbers, to taxa. Most of the specimens are described whereas others are simply listed under a particular name. Within rodents, Pelzeln (1883: 67–74) discussed ten species of native sigmodontines identified in Natterer’s collection and represented by specimens obtained at Ipanema: *Hesperomys* (*leucogaster*, *eliurus*, *pygmaeus*, *brachyurus*, *fuliginosus*, *russatus*, *physodes*, and *orobinus*), *Holochilus brasiliensis*, and *Oxymycterus nasutus*. Three of the *Hesperomys* (*brachyurus*, *fuliginosus*, and *orobinus*) and the *Oxymycterus* refer to akodontines (Ellerman, 1941; Musser and Carleton, 1993). Pelzeln’s descriptions of the Natterer specimens assigned to these names reflect the characters of short-tailed mice common to *Akodon*, *Bolomys*, and *Oxymycterus*. The taxa *brachyurus* and *fuliginosus* were even said to resemble *Lemmus arvalis*. Pelzeln’s description of the examples of *Holochilus* accords with our understanding of the genus, as we already noted. The descriptions of *eliurus* and *pygmaeus* clearly refer to mice much smaller in body size than *russatus*; those names are currently associated with a species of *Oligoryzomys* (Musser and Carleton, 1993). Measurements given by Pelzeln for *leucogaster* depict a rat larger than *russatus*, one with a very long tail (greater than

7 inches). Furthermore, Pelzeln describes the examples of *leucogaster* as very dark rats with rusty reddish gray upperparts and somewhat paler underparts. Of Pelzeln's ten accounts, only two bear significantly on the identity of Wagner's *russatus*. Pelzeln did not provide a description for *russatus* but did refer one of Natterer's specimens to it. His description of *physodes*, based on five specimens, recalls Wagner's description of *russatus*.

Our next step was to study Natterer's specimens. In 1992, G. G. Musser worked in the mammal collection at the Naturhistorisches Museum at Wien and studied some of Natterer's material, primarily the specimens assigned by Pelzeln to *leucogaster*, *eliurus*, *pygmaeus*, *russatus*, and *physodes*; below are results of his study.

''*Hesperomys leucogaster*'': Pelzeln (1883: 67) assigned four specimens (adults and young, all under Natterer's field number 75) to this taxon. Only three could be found in the collection at Wien: skins and skulls of two young adults (NMW B448 and B450) and an adult skin only (B449). All are examples of what is currently known as *Oryzomys ratticeps* (Musser and Carleton, 1993: 724). Pelzeln described the specimens as being large in body size with very long tails (see table 51), and having dark pelage over the upperparts and whitish gray venters; these traits are characteristic of *O. ratticeps*. These are not the specimens used by Wagner for his description of *russatus*; instead, they formed the basis for Wagner's *leucogaster*. We discuss the allocation of *leucogaster* and select a lectotype in our discussion of the *Oryzomys subflavus* group.

''*Hesperomys eliurus*'': Six examples from Ipanema and Itararé (all with Natterer's field number 54) were designated by Pelzeln (p. 68). Musser found six identified by number 54 (NMW B443, B444, B445, B476, B483, and B528), and all represent *Oligoryzomys eliurus* (Carleton and Musser, 1989: 73). There was also a seventh individual of *O. eliurus* (Natterer's field number 173; NMW 480), which Pelzeln had referred to *russatus*, an assignment we will discuss below.

''*Hesperomys pygmaeus*'': This taxon is represented by a single example (Natterer's field number 79; NMW B532) that Pelzeln (1883: 69) described as a small rat, much smaller than the animal Wagner described as *russatus*. The specimen is a juvenile *Oligoryzomys eliurus*.

''*Hesperomys russatus*'': Pelzeln (1883: 71) assigned number 173 (68) to this taxon, but his association is incorrect because the specimen does not fit Wagner's description of *russatus*, and it is clearly not the specimen Wagner had in front of him. First, number 173 (NMW 480) is a much smaller animal than the one Wagner described, as indicated by lengths of head and body, tail, hind foot, and ear (table 50). Second, the fur and skin color is too dark. Its dorsum is dark tawny with rusty highlights, not ''vibrant golden pale orange flecked with a little black,'' as Wagner described for *russatus*; the venter is whitish gray with a buffy tinge, not ''a beautiful yellow-white''; and the tail is brown on all surfaces, not ''darker on the dorsal surface.'' The chromatic traits (particularly the monocolored tail) and dimensions of number 173 are typical of *Oligoryzomys eliurus*, and the specimen is an adult of that species.

Other evidence indicates that number 173 cannot be the specimen described by Wagner. Barbara Herzig at Naturhistorisches Museum Wien sent us a catalog sheet made during Natterer's time on which information about 173 is entered. On the sheet is this note: ''bey H Prof Wagner zur Ansicht und hält er für ein Junges von H 53 Hesperomys physodes,'' which Herzig translated as, ''with Prof Wagner for investigation who regards it as a young of number 53 Hesperomys physodes.'' The only reference to *russatus* is another notation on the same page but written later and in ''Pelzeln's late handwriting'' (according to K. Bauer, retired head of the mammal collection at Wien; note in one of Herzig's letters), which Herzig translated as, ''probably Hesperomys russatus Wagner.'' Herzig agreed with us: ''Pelzeln was certainly wrong in taking 173 (68) for *russatus*.''

''*Hesperomys physodes*'': Four specimens in the collection at Wien bear Natterer's field number 53 and were described under *physodes* by Pelzeln (1883: 71). Pelzeln referred five specimens, which are recorded as *physodes* on a catalog page (photocopy sent to us by Herzig). The five had been sent in three lots (or transports). Later on the page, how-

TABLE 50

External Measurements (Inches) and Other Data Associated with Wagner's (1848) Description of *Hesperomys russatus* and the Specimens Listed by Pelzeln (1883) as *Hesperomys russatus* and *Hesperomys physodes*[a]

NMW catalog number	Natterer's field number	Age	Sex	LHB	LT	LHF	LE
Original description							
—	?	Adult	?	$6\frac{3}{4}$	$5\frac{3}{4}$	$1\frac{1}{2}$	$\frac{2}{3}$
"H. russatus"							
B480	173	Adult	Male	$4\frac{1}{2}$	$4\frac{3}{4}$	$\frac{7}{8}$	$\frac{1}{3}$
"H. physodes"							
B478[b]	53	Adult	Male	$6\frac{1}{2}$	$5\frac{5}{8}$	$1\frac{3}{8}$	$\frac{3}{4}$
B481	53	Adult	Male	$6\frac{3}{4}$	$5\frac{1}{8}$	$1\frac{3}{8}$	$\frac{7}{8}$
B477	53	Adult	Male	$6\frac{1}{4}$	$5\frac{1}{2}$	$1\frac{3}{8}$	$\frac{5}{8}$
B469	53	Young adult	Female	6	$6\frac{1}{4}$	$1\frac{3}{4}$	—

[a] Wagner's measurements are in zolls and linie, which we converted to inches; we used inches for all the specimens rather than converting again to millimeters. See footnote 9.

[b] The example we designate as lectotype for *Hesperomys russatus* Wagner (1848).

ever, there is a note referring to only four specimens (three males and one female stored in "window-drawer 67"), and Herzig could not find any additional specimen with the field number 53. In 1992, Musser studied the four examples, which by that time had been labeled "*Oryzomys subflavus*." All are specimens of what is currently called *Oryzomys intermedius*:

NMW B469, young adult female; March 16, 1819
NMW B477, adult male; March 25, 1822
NMW B478, adult male; May 25, 1822
NMW B481, adult male; May 20, 1821

"Type of *H. russatus* Wagner?" had been written on the catalog card for NMW B478 (Herzig noted that "The notation was probably written by A. Langguth, who visited the collection in the 1960s, according to Dr. K. Bauer").

Of all Natterer's "*Hesperomys*" from Ipanema, only the four specimens of "*physodes*" reasonably suggest Wagner's description of *Hesperomys russatus*, and one of these may have been the specimen he described. Two pieces of evidence support this supposition. First, near the bottom of the original catalog page, just below the notation about the four specimens stored in window-drawer 67, is a note that Herzig translated as, "with Prof. Wagner for investigation. Variety or new species."

Second, of the four specimens, the chromatic and dimensional characteristics of B478 match Wagner's description. External measurements of B478 are close to those given by Wagner (table 50), and it has the brightest upperparts of the four specimens and the whitest venter. The dorsal coat is tawny brown lightly flecked with black from head to rump and has bright ochraceous tones along the sides of head and body. The tone is certainly "vibrant" and the color could be described as "golden pale orange flecked with black." Most of the ventral coat appears to be solid white with very pale yellow highlights. The long whitish yellow portions of the hairs effectively suppress their gray bases; only on the neck and medial portions of the hind legs do the basal gray segments of the hairs show through, which produces a paler and duller cast to these regions compared with the cream highlights over most of the venter. Wagner's "beautiful yellow-white, becoming paler at the neck and the medial surfaces of the hind legs" is very descriptive. Tops of the feet are covered with white hairs but appear "dirty white" as described by Wagner because the underlying skin, which is grease-stained, shows through the hairs. Ears are scantily haired (''a hint of fine hairs'' in Wagner's words for *russatus*). The tail is also covered with very short hairs and is pale brown on its dorsal surface, unpigmented ventrally for two-thirds of its length, and is then mottled out to the tip. It closely resembles Wagner's description for *russatus*: ''nearly hairless, pale, and darker on the dorsal surface.''

We may never know how many specimens Wagner actually studied when he was writing his description of ''Die goldfalbige Scharrmaus.'' We do think it reasonable that Wagner had access at least to the four specimens collected by Natterer from Ipanema that Pelzeln later identified as *physodes*. We regard all four as syntypes of *Hesperomys russatus* Wagner (1848). Furthermore, one of them (NMW B478) so closely matches his description of *russatus* that we designate it as lectotype (Herzig wrote us that ''Altogether I also think that only B478 fits to Wagner's description of *russatus* . . .''), following the requirement of recommendation 73F (p. 151) in the *International Code of Zoological Nomenclature* (1985 edition):

> Where no holotype was designated and where it is possible that a nominal species-group taxon was based on more than one specimen, an author should proceed as though syntypes may exist and, where appropriate, should designate a lectotype rather than assume a holotype.

The lectotype consists of a skin (fig. 135) and skull (fig. 136). The skin is stuffed and, except for frayed ear margins, is in good condition. Most of the cranium and mandible is intact; portions of the basicranial and left auditory regions are missing, and the mandible lacks only tips of the coronoid processes. Measurements of skin and skull are listed in table 49.

It is now understandable why Wagner (1848) and Burmeister (1854) compared *russatus* with *physodes* Brants (not Olfers, 1818) and noted their close resemblance. The holotype of *physodes* Brants and the lectotype of *russatus* are not only similar in appearance, but they represent the same species.

Wagner's (1848) name *Hesperomys russatus* is older than Leche's (1886) *Hesperomys laticeps* var. *intermedia* and should be used for the species formerly known as *Oryzomys intermedius*. The name proposed by Wagner also has the advantage of being tied to a lectotype consisting of a nearly intact skull accompanied by a reasonably good skin, which exhibits the bright buffy orange or tawny upperparts so characteristic of the species. The lectotype of *intermedius* consists only of a cranium and mandible, which we document in the following account.

ALLOCATION OF *INTERMEDIUS*: Under the name ''*H. laticeps* Burmeister, var. *intermedia*,'' Leche (1886: 693) described a new taxon based on specimens from Taquara do Mundo Novo in southern Brazil. From the field, according to Leche's account, the specimens had been shipped to the Zoological Institute in Basel, initially reported upon by Hensel (1873) under the name ''*Hesperomys darwinii*?,'' and later sent to Leche by H. von Ihering with the permission of G. Schneider of the Institute. This material was just part of a large consignment of rodents that had been turned over to Leche for him to study and document through publication. Leche's initial enthusiasm for the project was dampened when he received the material because the specimens, having been improperly preserved and maintained, were in various stages of decomposition. As a result, his descriptions focused on cranial and dental features; skin characters were given less attention, and impressions of fur texture and color came mainly from illustrations made in the field. Leche thought the skulls of ''*H. darwinii*?'' exhibited characteristics intermediate to *Hesperomys laticeps* (sensu Burmeister, 1854) and *H. saltator* (species we know as *Oryzomys subflavus* and *O. laticeps*, respectively). Leche's account follows (translated by E. Brothers with our comments in brackets; the German version is reproduced in appendix R):

> The skulls of the nine specimens collected by von Ihering are in perfect concordance with Hensel's ''*H. darwinii?*.'' Thomas [Oldfield Thomas at the British Museum] tells me that they are not the same as Waterhouse's *Mus darwinii*; that species is a *Phyllotis*-form, while the present specimens (and Hensel's ''*H. darwinii*''), with which *H. laticeps* Lund is closely allied, belong to *Oryzomys*. At my request, the kind Mr. H. Winge has sent me three skulls from the Zoological Museum of the University of Copenhagen. Two of these (collected by Lund himself) are *H. la-*

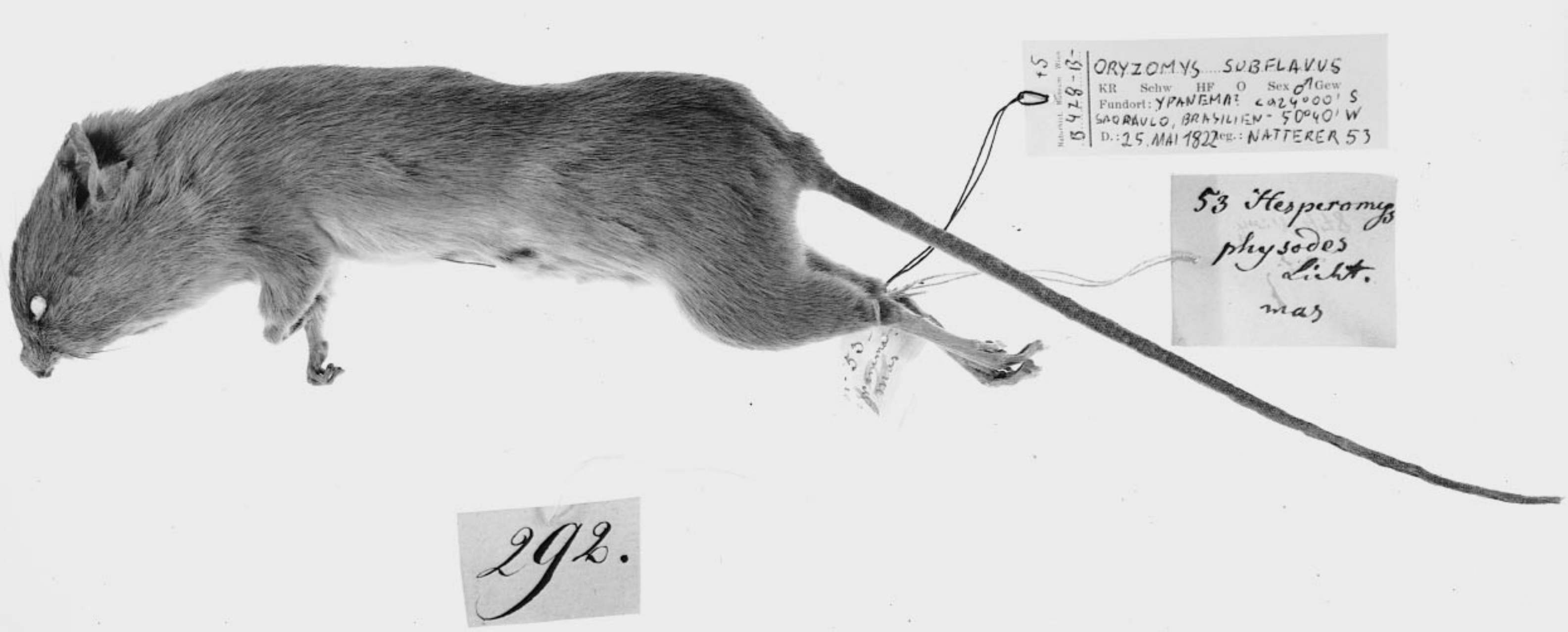


Fig. 135. Stuffed museum skin forming part of the lectotype of *Hesperomys russatus* Wagner (NMW B478), an adult male from Ipanema, Brazil. Some measurements are listed in table 49.

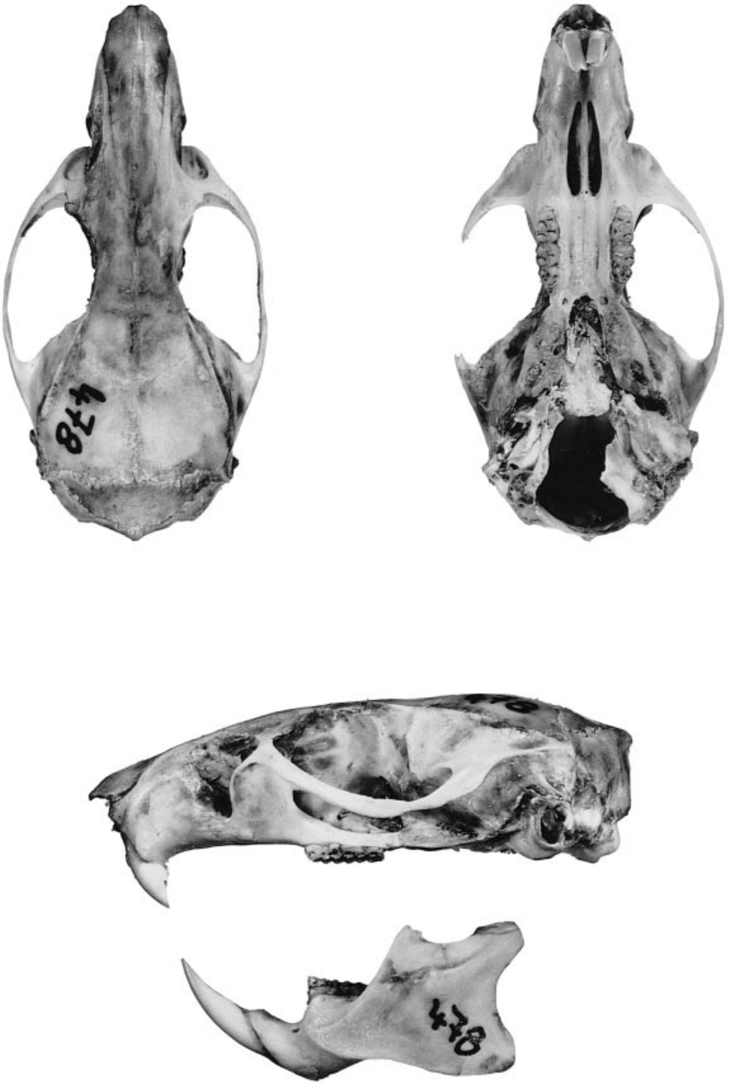


Fig. 136. Views of cranium and left dentary of the lectotype of *Hesperomys russatus* Wagner. The skin is portrayed in figure 135. The right zygomatic arch was damaged after the dorsal view was photographed. ×2. Measurements are listed in table 49.

ticeps Lund–Burmeister and the third (collected by Reinhardt) is identified as *H. saltator* [Lund–Burmeister's ''*laticeps*'' is the same as what is now known as *Oryzomys subflavus*, and Winge's *saltator* is synonymous with true *O. laticeps*; see our previous discussion in the section where we define our use of *laticeps*]. Winge has found that Lund's original specimen of *H. laticeps* is not the same as Burmeister's species of the same name. Its [the third skull's] form is in agreement with Lund's original, that is why Winge suggested the name *H. saltator*, while he applied the name *H. laticeps* in the sense used by Burmeister.

In looking at the last of these three skulls, it is apparent that it is like the specimens collected by von Ihering; both samples, just as ''*H. darwinii*?'' Hensel, occupy a middle point between *H. laticeps* and *H. saltator*.

1) In *H. laticeps* the supraorbital shelf, as Winge stressed, projects strongly; in my specimens of similar age the shelf is weaker, and in *H. saltator* it is absent entirely.

2) In *H. laticeps* the length of the upper molar row is slightly less than the incisive foramina; in the present specimens the upper molar row and the incisive foramina are about the same or the former is slightly

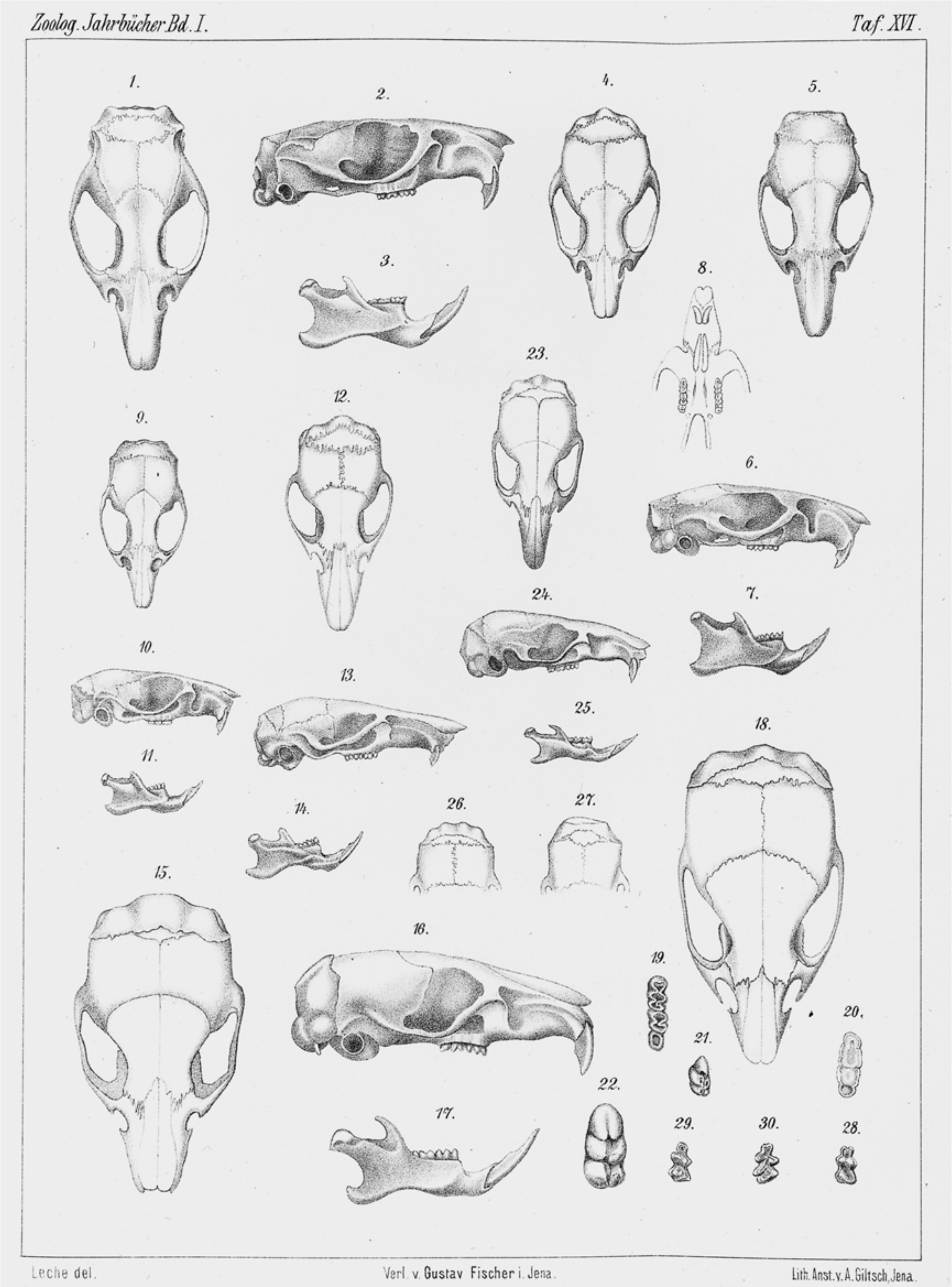


Fig. 137. Plate 16 from Leche (1886). Figures 5–8 illustrate Leche's new taxon *Hesperomys laticeps* var. *intermedia*.


1/12 1899 138.

Hesperomys laticeps, var.
intermedia, Leche ♂ (N 7498
Taquara do Mundo novo
Zool. Inst. G. Schneider in Basel.

Fig. 138. Views of cranium and dentary of the lectotype (UZM 7498) of *Hesperomys laticeps* var. *intermedia* Leche, an adult male from ‘‘Taquara do Mundo Novo,’’ Brazil. ×2. The label associated with the skull is reproduced at the bottom of the figure. Measurements are listed in table 49.

> longer, whereas in *H. saltator* the upper molar row is much longer than the incisive foramina.
>
> 3) The posterior margin of the rostrum ends as a point in *H. laticeps*, bluntly in *H. saltator*; both forms are seen in the present specimens.
>
> I here mention that I have only been able to examine three skulls of *H. laticeps* and *H. saltator*; I have not seen the skins and I am not familiar with these animals, so I tentatively venture that these forms are not different at the species level, but this should not be considered a final conclusion. It is only because von Ihering's series is so small that I am prevented from justifying it as a new species. The present skulls, in any event, are closer to *H. laticeps* than to *H. saltator*. Perhaps when the differences of both are presented in total I will be able to assert a definite place for *H. laticeps* Burm. var. *intermedia*.
>
> The greatest length of skull is 27 mm.
>
> The conformation of the skulls in other respects is evident in the illustrations.
>
> Length of head and body 131 mm.
>
> Length of tail 145 mm.
>
> Ears large, touching each other if some pressure is applied. Upper lip not split. Thumbs with nail on top. Tail faintly haired, tip without tuft. On the dorsal surface the hairs are gray at the bases, rusty red at the tips; on the ventral surface the bases are the same and the tips are dirty white.

Winge (1887: 151, third paragraph of footnote 5, part 10) had an opinion about Leche's new taxon (translated from the Danish by E. Brothers; the Danish version is reproduced in appendix L):

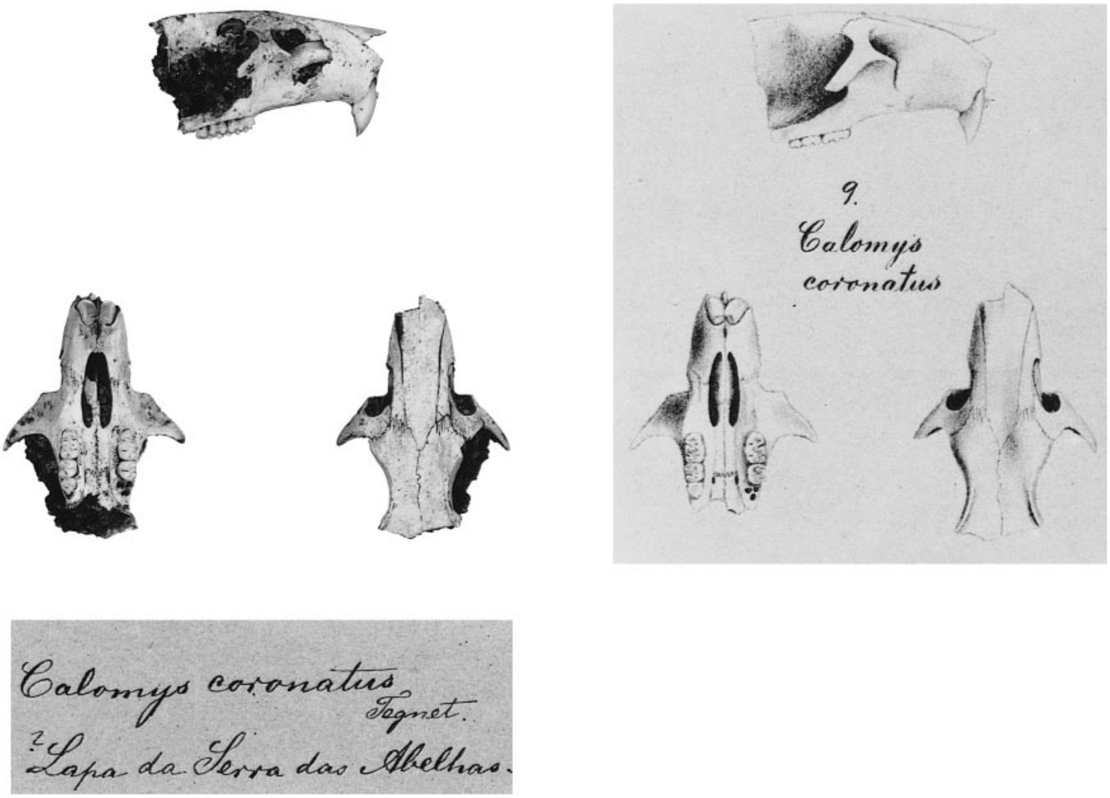
> Professor Leche has found some mice from southern Brazil which he considers to be intermediate, at least in regard to skulls, occupying a middle ground between *C. laticeps* and *C. saltator*; he has described it as ''*Hesperomys laticeps* var. *intermedia*.'' Leche borrowed skulls of both *laticeps* and *saltator* from the Copenhagen Museum to help with his determinations. He described three differences between *laticeps* and *saltator*: 1) conformation of the supraorbital shelf: in which var. *intermedia* is closest to *laticeps*; 2) dimensions of incisive foramina: here *intermedia* is also most similar to *laticeps*; in length of incisive foramina, *laticeps*, like so many other mice, shows considerable variation. But *saltator* is always remarkably short and broad, while *laticeps* is never so. 3) shape of the nasals: those of *intermedia* are sometimes like *laticeps*, sometimes like *saltator*. In this last respect, however, there is no difference between *laticeps* and *saltator*; the posterior edge of the nasals is highly variable in both, as is seen so often in mice. Professor Leche has surveyed and outlined the principal differences between skulls of *laticeps* and *saltator*; but he apparently was not aware of differences in the bones of the ear-drum, the wall of the nasal passage, the pit behind the lower incisors, differences in the ears, in the hands and feet (I have written a few words to him about differences in the feet as justification of the name *saltator*), etc. In fact, *laticeps* and *saltator* are two of the most distinct species in the genus *Calomys*. Leche's *H. laticeps* var. *intermedia* is not discernable from his descriptions and illustrations; perhaps it really is *laticeps*; it is not *saltator*.

Winge was correct about Leche's *intermedia* not being *saltator*, which we have shown is the same as *Oryzomys laticeps*. An illustration of the skull from the series of *intermedia* is included in Leche's report and is reproduced here in figure 137. The long rostrum and overall configuration of the cranium as viewed dorsally and its long and narrow incisive foramina resemble specimens in samples from Brazil that are morphologically close to *O. nitidus* and traditionally have been identified as *O. intermedius*; these cranial features are unlike the traits characteristic of *O. laticeps*.

The taxon Winge mistakenly recognized as *laticeps* is the species that is familiar to us as *O. subflavus*. Although Winge was uncertain whether Leche's description of *intermedia* referred to what he knew as *laticeps*, Leche's illustration is unlike crania of *O. subflavus*. Compared with the *nitidus*-like *intermedia*, examples of *O. subflavus* have, among many other distinguishing traits, pronounced supraorbital ridging and longer incisive foramina. The interorbit and ventral view of the cranium in Leche's illustrations are unlike *subflavus* and resemble *nitidus*-like specimens from Brazil. We are confident that at least one specimen in Leche's series—that on which the illustrations were based—is not an example of either *O. laticeps* or *O. subflavus*.

Leche did not designate a holotype for *intermedia*, nor did he identify by number the illustrated skull. All nine specimens in his original series can be considered syntypes. One of these ended up at the British Museum where it is unregistered and labeled as ''cotype'' of *O. intermedius*. Another (UZM 7498) is in Copenhagen, a skull that is labeled ''Hesperomys laticeps, var. intermedia, Leche; Taquara Do Mundo Novo; Zool. Inst. G. Schneider in Basel'' (fig. 138). We do not know whether this is the same skull figured by Leche, but it certainly came from his original series and had been given to Winge. That is the skull we designate as lectotype (measurements are listed in table 49).

ALLOCATION OF *CORONATUS*: Winge (1887: 51) described *coronatus* as a species of *Cal*-



Calomys coronatus
Tegnet.
?Lapa da Serra das Abelhas.

Fig. 139. **Left:** Holotype of *Calomys coronatus* Winge with label accompanying the specimen; collected by P. W. Lund at Lagoa Santa, Brazil. **Right:** Reproduction of Winge's (1887: pl. 3, fig. 9) original illustration. Measurements are listed in table 49.

omys (translation by S. Hoslett; original Danish version is provided in appendix S):

> Known only by means of the anterior part of a skull from Lapa da Serra das Abelhas.
>
> Its nearest relative is *C. laticeps*, which it differs in the following.
>
> Skull. Nasal passages are moderately strongly swollen posteriorly, especially to the sides; the swelling is seen on the frontals as 2 low bumps and shows also in the breadth of the maxillary in front of the incisors. A strong *Prc. supraorbitalis* like a rounded off ''list'' [molding or edging] along the orbital rim, about as in *Mus decumanus*, not shaped like a plate. The palate has no furrow posteriorly.

Winge also illustrated the fragment (pl. III, fig. 9 in his monograph, and reproduced here in fig. 139, along with a print of the partial cranium itself). He did not identity the piece as a type, but it becomes the holotype by monotypy as stated in article 73a(ii) of the *International Code of Zoological Nomenclature* (1985, third edition): ''If the nominal species-group taxon is based on a single specimen, either so stated or inferred in the original publication or demonstrated from evidence derived from outside the work itself, that specimen is the holotype by monotypy.''

Measurements of the partial cranium and molar row (table 49), along with its configuration, are consistent with size and shape characteristics of the anterior half of the cranium of other Brazilian specimens of *O. russatus*.

ALLOCATION OF *LAMIA*: Thomas (1901b: 528–529) remarked that *Oryzomys lamia* is ''A fairly large species, of a beautiful ochraceous-buff colour'' and described it in these words:

> Size rather less than in *O. subflavus*. Fur soft, close, and straight; hairs of back about 11 millim. in length. General colour a beautiful ochraceous buff, brilliant and clear on the cheeks, flanks, and hips, more or less

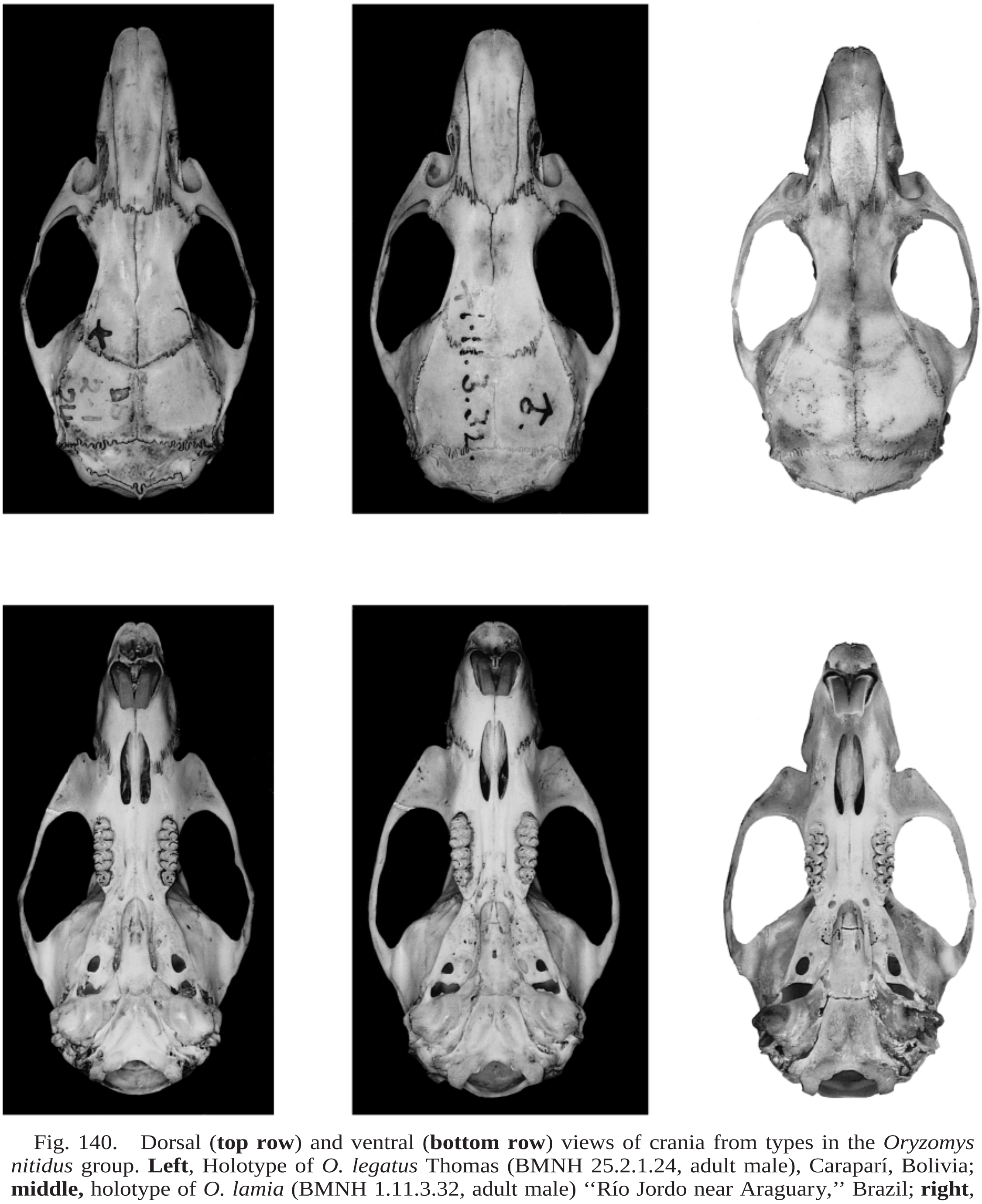


Fig. 140. Dorsal (**top row**) and ventral (**bottom row**) views of crania from types in the *Oryzomys nitidus* group. **Left**, Holotype of *O. legatus* Thomas (BMNH 25.2.1.24, adult male), Caraparí, Bolivia; **middle,** holotype of *O. lamia* (BMNH 1.11.3.32, adult male) ''Río Jordo near Araguary,'' Brazil; **right**, paratype of *O. kelloggi* (AMNH 203073, adult male), Além Paraíba, Brazil. ×2. Measurements are listed in table 49.

Fig. 141. Lateral views of same crania depicted in figure 140 on opposite page. **Upper left,** Holotype of *O. legatus*; **upper right**, holotype of *O. lamia*; **lower center,** paratype of *O. kelloggi*. ×2.

> lined with black on the back; in the oldest and brightest specimens the middle area of the back is lined and coloured about as in *O. flavicans* (though of a less reddish tinge), but the bright ochraceous buffy of the flanks is unrivalled in any species known to me. Under surface sharply defined white, the bases of the hairs slaty, except just on the chin and scrotal region, where the hairs are wholly white. Head like back, top of muzzle slightly greyer. Ears large, finely haired, pale brown, contrasting but little with the head. Front of fore limbs like body to wrist, remainder and whole upperside of hands white; hind limbs buffy above, the upper surface of the feet also tinged with buffy. Tail nearly naked, the hairs excessively short and fine; unusually finely scaled, the rings running nearly 20 to the centimetre; above brown, beneath white, darkening towards the tip.
>
> Skull heavily built, with broad muzzle and broad interorbital region, whose edges are sharply square or have a fine beading along them, but are without overhanging ridges. Palatal foramina rather longer than the molar series, not widely open, their posterior end some distance in front of m^1. Palate ending some way behind m^2.

‘‘This beautiful species,’’ Thomas explained, ‘‘seems widely different from any *Oryzomys* hitherto described from South Brazil. Perhaps its nearest ally is *O. intermedius*, Leche, which is, however, much less brilliantly coloured, and has a slenderer skull with narrower nasals and narrower interorbital region.’’

Thomas correctly assessed the relationships of *lamia*. Characteristics of the holotype, particularly the cranium (figs. 140, 141), place it with the species we define as *O. russatus* (see fig. 114 and discussion in the account of *O. nitidus*).

ALLOCATION OF *LEGATUS*: Diagnosed by Thomas (1925: 577–578) as ‘‘Near *O. intermedius* of S. Brazil,’’ the description of his new species, *Oryzomys legatus*, was short:

> General external appearance quite as in specimens from São Paulo of *O. intermedius* and of *O. boliviae* of North Bolivia, the upper surface of the same dark-lined buffy, with brighter buffy sides and white belly, the hairs of which are grey basally. Ears large, brown. Hands and feet white. Tail long, finely scaly, brown above, lighter below, especially proximally, but not sharply bicolor.
>
> Skull very like that of *O. intermedius*. Zygomata more spread out behind, instead of being evenly curved outwards. Nasals less pointed behind. Interorbital region broader. Palatal foramina rather shorter. Incisors unusually opisthodont; angle of type 61°.

The holotype was collected in southern Bolivia. Thomas continued:

> This appears to be the furthest south recorded, in the western half of S. America, of any of these large species of *Oryzomys*, the animal seeming to be a representative in S. Bolivia of the Brazilian *O. interme-*

> *dius*. In N. Bolivia there is already an ally of that animal—*O. boliviae*,—but the present form is even more like *intermedius*, from which, however, it differs by the different curvature of its zygomata, and, chiefly, by its broader interorbital region, this being in *boliviae* quite the same as in the Brazilian species.

Thomas perceptively estimated the affinities of *legatus*; in our analyses it does represent the Brazilian *Oryzomys russatus* in southern Bolivia and northern Argentina (see fig. 114 and comparisons in the account of *O. nitidus*).

ALLOCATIONS OF *KELLOGGI* AND *MOOJENI*: Our placement of the two taxa named by Ávila-Pires (1959a, 1959b) with *O. russatus* is provisional because we have not examined the holotypes. However, we have studied two paratypes (skins and skulls) of *kelloggi* (AMNH 203073, figs. 140, 141; USNM 332452) and a paratype of *moojeni* (AMNH 203074) that were sent by Ávila-Pires (1963: 176–177) to the American Museum of Natural History and the National Museum of Natural History. Body size, coat coloration, and cranial and dental features of all three specimens are characteristic of *O. russatus*. Description of the holotype of *kelloggi* (Ávila-Pires, 1963: 176) is consistent with our definition of *O. russatus*, especially measurements of the skull and dentition (for example, Ávila-Pires provided these measurements: ONL = 35.4 mm, ZB = 18.4 mm, IB = 5.3 mm, LIF = 5.9 mm, and length of molar row is 5.0 mm; compare these with measurements in table 49 and appendix E), and we are confident about our identification of that specimen, even though we know it only from the published original description.

The holotype of *moojeni* reportedly has a long molar row (5.7 mm; 5.5 mm is the longest we measured for *O. russatus*); otherwise, most measurements of the holotype, as well as its coloration (Ávila-Pires, 1963: 177), are within the range of variation we record for Brazilian samples of *O. russatus*. Ávila-Pires (1960) treated *moojeni* as a subspecies of *Oryzomys ratticeps*, but the dimensional contrasts he reported (p. 6; note especially the values from lengths of head and body, tail, hind foot, cranium, and molar row) between samples of *O. r. ratticeps* and *O. r. moojeni* are similar to those that separate the larger bodied, longer tailed *O. ratticeps* from the smaller *O. russatus*. We assign *moojeni* to synonymy with *O. russatus* as we know it from a paratype (table 49) and measurements of the holotype and other specimens reported by Ávila-Pires (1959b, 1960).

Morphometric traits of the paratypes of *kelloggi* and *moojeni* cluster with our samples of *O. russatus* and the other types discussed here (fig. 114).

SCIENTIFIC NAMES ASSOCIATED WITH SPECIES IN THE *ORYZOMYS SUBFLAVUS* GROUP

This assemblage consists of the two species that Musser and Carleton (1993) recognized as *O. subflavus* and *O. ratticeps*. Both occur in eastern Brazil, northern Argentina, and eastern Paraguay where they overlap the geographic distributions of either *O. nitidus* or *O. russatus*; *O. subflavus* is also found in eastern Bolivia where it narrowly overlaps the Bolivian range of *O. yunganus* and is broadly sympatric with *O. nitidus*. Neither *O. subflavus* nor *O. ratticeps* has been explicitly regarded as a member of the former *O.* ‘‘*capito*’’ complex, but some of the scientific names associated with each are based on vague descriptions that could as well apply to members of the *O. nitidus* group, particularly to *O. russatus* or to *O. nitidus*. We were not interested in taxonomically revising *subflavus* and *ratticeps*, but we necessarily examined types and original descriptions of all scientific names associated with the two species. Identifying name-bearing specimens and series that are associated with the *O. subflavus* group, as well as designating a neotype and lectotypes where necessary, would help stabilize the nomenclature of species in the former *O.* ‘‘*capito*’’ complex and those of the *O. subflavus* group. Results of our investigations are reported below.

ORYZOMYS SUBFLAVUS

Mus vulpinus Lund (1840 preprint of 1841: 279). TYPE LOCALITY: Brazil, Estado do Minas Gerais, Lagoa Santa (locality 198 in gazetteer for *O. russatus*). LECTOTYPE: UZM 282 (skin and incomplete skull; measurements listed in table 51), an adult male collected by P. W. Lund.

Hesperomys subflavus Wagner (1842: 362). TYPE LOCALITY: Brazil, Estado do Minas Gerais, Lagoa Santa (restricted by Cabrera, 1961: 396). HOLOTYPE: ZSM 167/249 (mounted skin and incomplete skull; measurements listed in table 51), a young adult male.

Mus vulpinoides Schinz (1845: 193). A renaming of Lund's *Mus vulpinus*; the name attaches to the lectotype, UZM 282.

Nomenclatural Issues

ALLOCATION OF *VULPINUS*: *Oryzomys subflavus* was first described by Lund (1840: 279) under the name *Mus vulpinus* in a section in which the ''remaining species, all of which belong here, I have separated into two groups to facilitate study, since tails are either shorter or longer than bodies;'' the account of *vulpinus* is in the group of species with tail longer than body (translated by E. Brothers; see appendix T for a reproduction of the Danish text):

> *Mus vulpinus*, 12″ 6‴ long, of which the body is 5′4‴ and tail is 7′1‴, is characterized by its long-haired pelt, of which the color is vibrant rust-red above, and white with a touch of rust-yellow below.[9]

The proper application of *vulpinus* to specimens has been entangled with *laticeps*, *saltator*, and *subflavus*, as explained previously in the account allocating *saltator* to *laticeps*. The link between *vulpinus* and the actual species to which Lund's name applies has never been adequately documented, and because his description is so vague, the allocation of *vulpinus* must rely on examination of the specimen or specimens he studied. Unfortunately, Lund did not designate a holotype in his description or indicate how many specimens he examined. Fortunately, Lund's material from Lagoa Santa is preserved and was studied by Winge, who matched Lund's specimens to descriptions by noting that the sample consisted of one or more ''Expl'' of a particular taxon. At Copenhagen, A. L. Gardner located three specimens from Lagoa Santa (UZM 282, 283, and 284) marked as Lund's 1st, 2nd, and 3rd ''Expl,'' respectively, of *Mus vulpinus*, none of which had date of collection. A label associated with each specimen has ''*Calomys laticeps* Lund'' on it in Winge's handwriting (see our account allocating *saltator* to *laticeps* for the explanation of why Winge applied the name *laticeps* to examples of *vulpinus*/*subflavus*). All three exhibit the cranial and dental morphologies associated with the species currently identified as *Oryzomys subflavus* (figs. 142–144): moderately long rostrum, prominent ridges or shelves overhanging the supraorbital region, long and narrow incisive foramina, short bony palate, no alisphenoid struts (confluent foramen ovale accessorius and masticatory–buccinator foramen; see Carleton and Musser, 1989: 30), a derived arrangement of the cephalic arterial circulation that is apparently identical to the pattern found in *O. palustris* (Carleton and Musser, 1989: 38; Voss and Carleton, 1993), mesopterygoid fossa with short and slitlike sphenopalatine vacuities, second upper molar with labial and medial fossettes, and second lower molar with short hypoflexid. Crown length of the upper molar row of the ''1st Expl'' (UZM 282) is 5.5 mm, which is within the range of *O. subflavus* but is shorter than that typical of *O. ratticeps*.

Although F. W. Braestrup told Gardner that the specimens marked ''1^{ste} Expl.'' by Winge were regarded as types in the Copenhagen Museum and are so indicated in the catalog, no holotype of *vulpinus* has ever officially been identified. We consider all three ''Expl'' to be syntypes and designate UZM 282, the ''1st Expl,'' as lectotype of *Mus vulpinus* Lund (1840 preprint of 1841 text: 279) following recommendation 73F (p. 151) in the *International Code of Zoological Nomenclature* (1985 edition). The specimen is an adult male, consisting of a skin (with dry phallus) and incomplete skull; some cranial and dental measurements are listed in table 51.

Lund's (1840) *Mus vulpinus*, although published earlier than Wagner's (1842) *Hesperomys subflavus*, should be listed in the synonymy of *Oryzomys subflavus* (as done by Trouessart, 1904: 421; Gyldenstolpe, 1932: 21; Ellerman, 1941: 353; Ávila-Pires, 1959c: 28; and Cabrera, 1961: 396), but is not an available name because it is preoccupied by *Mus vulpinus* Brants (1827: 137; illustrated by Lichtenstein, 1830: color plate 33, fig. 2), which is a form of *Holochilus*. Wagner's (1842) *Hesperomys subflavus* therefore becomes the oldest available name for the species described by Lund as *Mus vulpinus*.

Identity of *subflavus*: We were concerned about the true identity of Wagner’s *subflavus* for several reasons. The holotype has never been clearly described or illustrated. Early accounts provide scanty and undiagnostic information. Both of Wagner’s (1842, 1843) descriptions, for example, recalled *Oryzomys russatus* rather than characteristics of the species currently recognized as *O. subflavus*. Burmeister (1854) considered Wagner’s *subflavus* to be the same as Lund’s (1840) *Mus laticeps* and described a rat that also seems more like *O. russatus* or some other species included in the former *O.* ‘‘*capito*’’ complex. We needed to determine whether Wagner’s *subflavus* applied to a member of that complex.

Wagner’s (1842: 362) original diagnosis of ‘‘*Hesperomys subflavus*’’ is short: ‘‘Hesperomys supra bruneo-flavidus, subtus albidus, pedibus sordide albidis; cauda longitudine corporis, squamata, raripilosa. Corpus 6″, cauda 6″. Brasilia.’’ He provided a longer description in 1843 (p. 534), which E. Brothers translated as follows (see appendix U for the original version in German):

> 24. H. subflavus Wagn. The light dun ‘‘Scharrmaus.’’ H. Ratto somewhat smaller, brownish yellow, whitish venter, feet dirty white; tail as long as the body, scaly, sparsely haired [originally presented in Latin].
>
> The external appearance is entirely ratlike, including the tail, which is finely scaled and has isolated small hairs. The ears are medium-sized, covered with fine small hairs on the outside and inside, especially on the posterior edge of the latter. The teeth are of typical shape. The feet are delicate. The color of the upperparts is brownish-yellow, sprinkled with black along the back and the top of the head; the underside is whitish. All the hairs of the upperparts are slate-colored on the lower half, loamy yellow on the top half; commingled along the spine are many black hairs. On the underside, too, the hairs are slate-colored against the ground. A gray color predominates the front of the snout. The moustache is black, a few hairs have whitish tips. The longer hairs on the posterior edge of the inside of the ears is rust yellow. The feet have whitish hair, more sullied on the hind feet; the soles are naked. The tail is a proper rat tail.

Body	6″	0‴	Ear	0″	8‴
Tail	6	0	Hind foot	1	1½

> According to the statements of Brant’s natural history specimen providers, the habitat is Brazil.[9]

Cabrera (1961: 396) restricted the type locality: ‘‘Brasil, lo que se puede restringir a Lagoa Santa, estado de Minas Gerais, si *subflavus* es, como generalmente se admite, sinónimo de *vulpinus* Lund (no Brants).’’

Wagner’s (1843) second and longer account of *subflavus* is still not useful for identifying the taxon. Fortunately, A. L. Gardner had visited the Zoologische Staatssammlung München in the late 1970s and studied the holotype of *Hesperomys subflavus*. It is a mounted skin from which the skull has been removed; number 167 is associated with the skin and number 249 with the skull. Of the skin, Gardner noted only that the underparts were ‘‘white tipped gray.’’ The skull is incomplete: the posterior end of the braincase is missing and the right zygomatic arch is broken. Selected measurements are listed in table 51. The cranium lacks a sphenofrontal foramen and squamosoalisphenoid groove, has wide overhanging supraorbital shelves, and each second upper molar has a medial fossette, a combination of traits that is uncharacteristic of *O. russatus* (see our account of that species) but is diagnostic for Brazilian and Bolivian *Oryzomys* currently identified as *O. subflavus* (see figs. 142–144). The two species are also easily distinguished by skin and fur characters. Compared with examples of *O. russatus*, specimens of *O. subflavus* have conspicuously longer tails (table 37), darker tawny brown upperparts (without the bright buffy and ochraceous tones so characteristic of *O. russatus*), buffy dorsal surfaces of front and hind feet (white in *O. russatus*), sparse ungual tufts of hairs that do not extend beyond tip of the claw (thick tufts of long hairs extend beyond and conceal the claws in *O. russatus*), and much darker venters that are either buffy gray, grayish white, or some combination between those extremes (whitish gray or bright white with a hint of pale gray suffusion in *O. russatus*). Wagner’s *subflavus*, judged by morphology of the holotype, is not an example of *O. russatus* or of any other taxon included in the former *O.* ‘‘*capito*’’ complex.

Allocation of *vulpinoides*: In addition to *Mus vulpinus* (Lund, 1840), we know of only one other scientific name that should be listed in the synonymy of *O. subflavus*[12]. Schinz (1845: 193) proposed *Mus vulpinoides* to replace Lund's *Mus vulpinus* because it is preoccupied by Brants (1827) *Mus vulpinus*.

Remarks: We discovered that Thomas (1901b: 528) had previously provided the same synonymy as indicated above. In a report on mammals collected by A. Robert from the ''Rio Jordão'' (locality 199 in gazetteer for *O. nitidus* group), Thomas identified one specimen as *Oryzomys subflavus*, which

> closely agrees with an example from Lagoa Santa, determined by Winge as ''*Calomys laticeps*,'' the *Mus vulpinus* of Lund, *nec* Brants, renamed *vulpinoides* by Schinz; therefore a topotype of that species. But it also precisely agrees with Wagner's ''*Hesperomys subflavus*,'' described two years before Schinz's name was published, of which I have examined the type in the Munich Museum. So close is the agreement that my measurements of the typical skull might almost have been taken on Mr. Robert's specimen. The name *vulpinoides* will therefore become a synonym of *subflavus*.
>
> The relationship of this species to *O. anguya*, Desm., remains to be settled when topotypes of the latter are obtained from Paraguay.

Oryzomys subflavus, as its morphological limits are currently understood, is a distinctive species found in eastern Brazil from the states of Ceará, Pernambuco, Alagoas, and Bahia in the north (Mares et al., 1981a; Streilein, 1982), south through the Federal District (Mares et al., 1986; Nitikman and Mares, 1987; Alho et al, 1986; Mares et al., 1989) and Minas Gerais (Fonseca and Kierulff, 1989; Stallings, 1989; Ávila-Pires, 1959c; Paglia et al, 1995), to São Paulo (Olmos, 1991; Vieira, 1997) and the Pantanal region in Mato Grosso do Sul (Alho et al., 1987); Alho (1982) also recorded the species from the states of Rio Grande do Norte, Paraíba, Sergipe, and Goiás. The distribution includes eastern Paraguay (Myers, 1982) and the north-central and eastern parts of Bolivia (Anderson, 1997).

Although often cited in faunal reports and represented by a considerable number of specimens in institutional collections, modern inquiry into variation of morphological and other traits among geographic samples of what has been identified as *Oryzomys subflavus* has yet to be undertaken. Results of such a revisionary study would do much to provide a sharper definition of the species and reveal any appreciable pattern of geographic variation.

ORYZOMYS ANGOUYA

Mus angouya Fischer (1814: 71), based on Azara's (1801: 86) ''Rat troisième, ou Rat Angouya.'' NEOTYPE: UMMZ 124201 (skin, fig. 145; skull, figs. 146, 147; intact dentition, fig. 148; carcass preserved in fluid; measurements listed in table 51), a young adult male collected August 22, 1976 by P. Myers. TYPE LOCALITY: Paraguay east of the Río Paraguay, Departamento de Misiones, 2.7 km (by road) N San Antonio (locality 6 on map in Myers and Carleton, 1981: 2).

Mus buccinatus Olfers (1818: 209). The second oldest and available name applied to Azara's ''Rat troisième, ou Rat Angouya.''

Mus angouya Desmarest (1819: 62). A third name based only upon Azara's description of ''Rat troisième, ou Rat Angouya.''

Hesperomys leucogaster Wagner (1845: 147). TYPE LOCALITY: Brazil, Estado do São Paulo, Ipanema (locality 182 in gazetteer for *O. russatus* and fig. 79). LECTOTYPE: NMW B450 (skin and skull, figs. 145–147; measurements listed in table 51), a young adult female collected June 14, 1821 by J. Natterer.

Hesperomys ratticeps Hensel (1872: 36). TYPE LOCALITY: Brazil, Estado do Rio Grande do Sul. LECTOTYPE: ZMB 47721 (skull, figs. 146, 147; body in fluid; measurements listed in table 51), a young (juvenile–young adult) female.

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[12] Hershkovitz (1960: 543), in another instance of taxonomic revision by footnote, stated that

> ''*Oecomys*'' *catherinae* Thomas is a synonym of *Oryzomys subflavus*. ''*Oecomys*'' *rex* Thomas, 1910, of British Guiana, is also a member of the same species but probably subspecifically distinct. The name, however, clashes with ''*Calomys*'' [=*Oryzomys*] *rex* Winge, 1888. Because of the homonymy, the name of the form described by Thomas may be changed to *Oryzomys subflavus regalis* (new name).

A. L. Gardner and G. G. Musser independently studied the holotypes of *catherinae* and *rex* at the British Museum; both are examples of *Oecomys*, not of *Oryzomys subflavus*, an identification reported by Musser and Carleton (1993: 716–717, 725) that will be documented in a forthcoming revision of *Oecomys* (Musser et al., unpubl. MS). The geographic range of *O. subflavus* does not include the Guianas; its often-cited occurrence there (by Stallings, 1988, for example) is based exclusively on Hershkovitz's incorrect allocations of *catherinae* and *rex*.

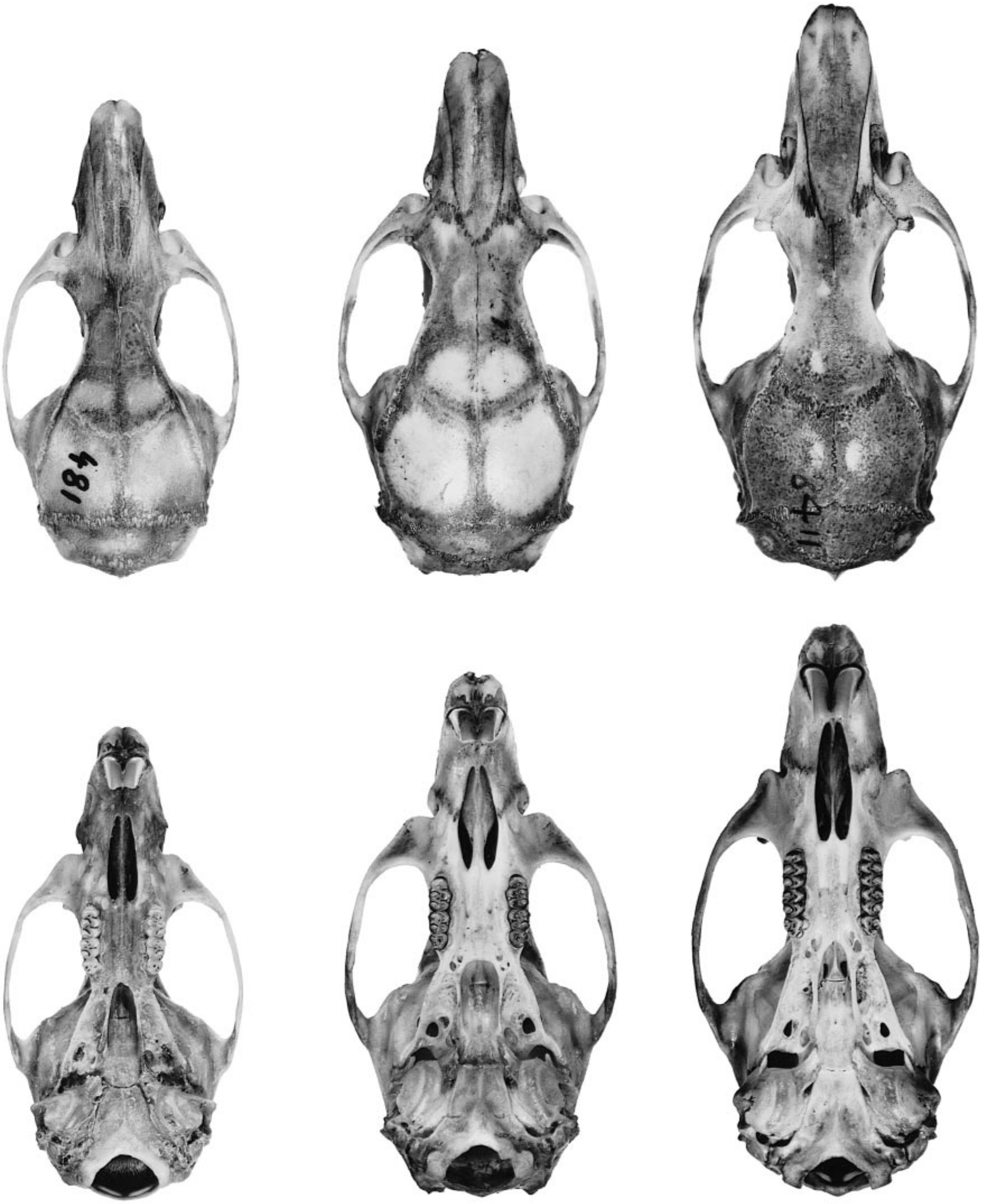

Fig. 142. Dorsal (**top row**) and ventral (**bottom row**) views contrasting the cranium of *O. russatus* (**left,** NMW B481, an adult male from Ipanema, Estado de Minas Gerais, Brazil) with those of *O. subflavus* (**middle**, AMNH 134712, an adult female from Maracajú, Estado de Minas Gerais, Brazil), and *O. ratticeps* (**right**, AMNH 248411, a young adult male from 5 km [by road] ENE Ayolas, Departamento de Las Misiones, eastern Paraguay). ×2. Measurements are listed in tables 49 and 51.

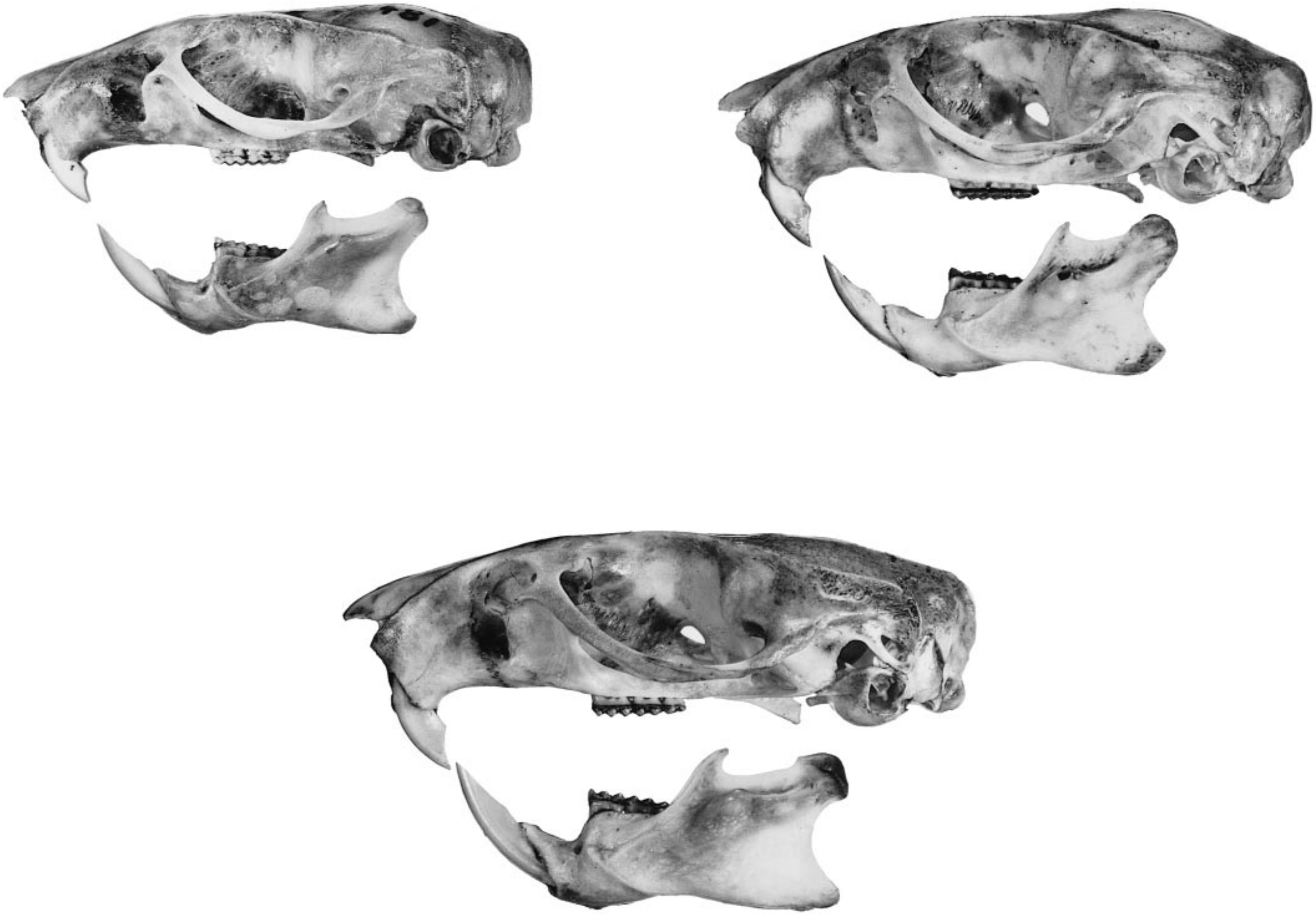

Fig. 143. Lateral views of crania and left dentaries from the same specimens portrayed in figure 142 on opposite page. **Upper left** *subflavus*; **upper right**, *O. russatus*; **lower center**, *O. ratticeps*

Fig. 144. Occlusal views of upper (left member of each pair) and lower (right member of each pair) molar rows of *O. subflavus* (left pair, AMNH 134566, Anápolis, Brazil; CLM1–3 = 5.2 mm, clm1–3 = 5.4 mm) and *O. ratticeps* (AMNH 80393, Rio Caparaó, Brazil; CLM1–3 = 6.4 mm, clm1—3 = 6.6 mm). The occlusal patterns in both species, especially those exhibited by the upper and lower second molars, are similar those seen in members of the *O. nitidus* group. Refer to the illustrations of those teeth in figures 81 and 104; also see figures 29–32.

Calomys rex Winge (1887: 50). TYPE LOCALITY: Brazil, Estado Minas Gerais, Lagoa Santa (see locality 198 in gazetteer for *O. russatus*). No type designated; based upon cave fragments in paleontological collections of UZM, collected by P. W. Lund.

Oryzomys ratticeps tropicius Thomas (1924: 143). TYPE LOCALITY: Brazil, Estado São Paulo, Piquete (locality 187 in gazetteer for *O. russatus*), 700 m. HOLOTYPE: BMNH 1.6.6.34 (skin and skull), an adult male collected January 26, 1901 by A. Robert.

Oryzomys ratticeps paraganus Thomas (1924: 144). TYPE LOCALITY: Paraguay, Departamento de Paraguarí, Sapucaí (Sapucay on specimen tag; 25°40′S/56°55′W, Paynter, 1989: 43). HOLOTYPE: BMNH 4.1.5.24 (skin and skull), an adult female collected August 28, 1903 by W. Foster.

Nomenclatural Issues

The ‘‘Rat troisième, ou Rat Angouya’’ was the common name given to one of the species of sigmodontine rodents Felix de Azara described in his *Essais sur l’histoire naturelle des quadrupèdes de la province du Paraguay,* published in 1801 (pp. 86–90). Azara’s description of the third rat is the basis for three scientific names: *Mus angouya* Fischer (1814: 71), *Mus buccinatus* Olfers (1818: 209), and *Mus angouya* Desmarest (1819: 62). Azara had also described the ‘‘Rat second, ou Rat à grosse tête,’’ for

TABLE 51

Measurements (mm), Age, and Sex of Types and Two Additional Specimens in the *Oryzomys subflavus* Group

(The two other specimens are not types, only exemplars of each species illustrated in figs. 142 and 143.)

	Types						Exemplars[g]	
	O. subflavus		*O. angouya*				*Oryzomys*	
	vulpinus[a] UZM 282	*subflavus*[b] ZSM 167/249	*angouya*[c] UMMZ 124201	*leucogaster*[d] NMW B450	*ratticeps*[e] ZMB 47721	*tropicius*[f] AMNH 36497	*subflavus* AMNH 134712	*angouya* AMNH 248411
Age	Adult	Yg adult	Yg adult	Yg adult	Juv–yg adult	Adult	Adult	Yg adult
Sex	Male	Male	Male	Female	Female	Male	Female	Male
LHB	?	±166	185	±170	?	155	170	194
LT	?	±160	210	±210	?	210	215	201
LHF	?	32	40	40	34	37	40	40
LE	?	17.1	25	22	?	22	21	—
ONL	—	—	40.5	39.7	32.2	40.5	40.0	43.5
ZB	19.7	±16.8	21.1	20.7	17.0	20.7	20.4	21.5
IB	6.6	5.7	6.0	4.9	5.4	5.2	6.6	5.5
LR	?	?	12.4	11.1	?	12.6	12.2	13.5
BR	7.5	6.8	8.0	7.3	6.4	7.4	7.7	8.0
LB	—	—	14.6	13.1	13.2	14.3	15.0	15.1
HBC	?	—	10.5	11.3	?	11.0	10.9	11.8
BZP	4.2	3.1	5.0	5.4	3.2	4.4	4.2	5.0
LD	?	?	10.4	10.1	?	10.3	9.9	10.5
LBP	5.8	5.9	6.6	7.6	5.6	7.1	6.7	7.7
PPL	?	—	15.0	14.8	?	14.6	13.8	16.1
LIF	?	?	8.6	8.4	?	8.5	7.5	8.6
BIF	?	?	2.9	3.2	?	2.5	2.9	2.7
CLM1-3	5.5	5.0	6.1	6.4	5.9	6.1	5.5	6.4
BM1	?	?	1.7	1.9	?	1.7	1.7	1.8

[a] Lectotype, based on the "1st Expl" of *Mus vulpinus* Lund (1840 preprint of 1841 text). Measured by A. L. Gardner.

[b] Holotype. Measured by A. L. Gardner.

[c] Neotype. Values for skin measurements obtained from fresh specimen in the field by P. Myers; skull and dentition measured by G. G. Musser.

[d] Lectotype. Measured by G. G. Musser. Values for external dimensions were obtained from the stuffed skin (fig. 145).

[e] Lectotype. Measured by A. L. Gardner. The numbers, 24643 = B656, are also associated with the skull.

[f] Paratype (formerly BMNH 1.6.6.33). Lengths of head and body, tail, and ear taken from original label attached to museum skin; length of hind foot as well as cranial and dental dimensions measured by G. G. Musser.

[g] Fresh specimens were measured in the field and values for skin measurements are taken from labels attached to skins; G. G. Musser measured the crania and toothrows.

which Fischer (1814) had provided the name *Mus megacephalus*, the oldest name for the species usually known as *Oryzomys capito*. Did Azara characterize another member of the group we include in the former *Oryzomys* "*capito*" complex, such as the species we have diagnosed as *O. nitidus*, which we document from Paraguay? If he did, then Fischer's *angouya* would be the valid name to use. Furthermore, additional scientific names have been considered synonyms of Olfers' *buccinatus* (Hershkovitz, 1959: 347). Do any of these names actually apply to the species occurring in eastern Paraguay that we diagnose as *O. nitidus*, or to *O. russatus* in Brazil? To answer these questions we first appraised Azara's description of the "Rat troisième, ou Rat Angouya." Below is the English version of Azara's account (translated by Mary Ellen Holden; the description in French, which was originally translated from Spanish by M.L.E. Moreau-Saint-Méry, is reproduced in appendix V; our comments are in brackets):

THIRD RAT OR *ANGOUYA* RAT

This is the name which, among the Guaranis, includes all the rats, the mice and the animals that resemble them in some respects; as with my last Micourés, for example. Nevertheless I give it to this particular rat, because, in groups of animals, that are as numerous as those of the rat, it is impossible to assign a name that characterizes each species. One is therefore compelled to hazard some not very expressive names. Independent of the impossibility of giving characteristic names to rats, there is yet another [difficulty] that is not of lesser consequence, that of discerning characters that distinguish one species from another; because often the species vary, although the proportions are nearly the same in the principal measurements, as the preceding species and this one come into contact; and while one of the species is larger than the other, there still remains some doubt, since this difference could possibly be due to age.

The forms that are found also, in certain circumstances, are so much alike, that one cannot distinguish them without extreme difficulty, and moreover it becomes impossible to succeed at it, when one only has a few specimens, and at such long intervals of time, that the ideas, by which the observer believed to be able to grasp the connection at first glance, are fading.

With respect to the types that then furnish the characters, he likewise meets many resemblances and identities in species of the same group, aside from this, to understand these characters, it is essential to know the age, and that they vary according to climate and particular circumstances. I have met with all of these difficulties, and they have not allowed me to assure with absolute certainty, that this third rat is different from the second, and I am limited to say that they seem different to me, in my defense, not only based upon my first examination and on the differences found as I compared the two descriptions, but also on the fact that the preceding rat [second rat or broad-headed rat] appeared to me to be an adult, and smaller; and the fact that it lives among the people of Saint-Ignace, and that the current rat was taken from a distance of 50 leagues[13] [approximately 240 km] from there, on the slope of a mountain gorge inhabited by the tribe of Atira, with another smaller individual of this species.

Length, 11½ inches (31 centimeters).

Tail 6 inches (16 centimeters), and one could call it bald, although it has short hair as is common in rats; at its base its circumference is 9½ inches (2 centimeters).

Anterior height, 2¼ inches (6 centimeters); posterior, 3½ inches (9⅓ centimeters).

The forehead is somewhat woolly, and from the base of the ear to the point of the snout, it measures $1\frac{2}{12}$ inches (3 centimeters). The eye is somewhat close to the ear, and is situated $\frac{6}{12}$ inches (1⅓ centimeters) from the other eye. The snout is a bit sharply pointed and not naked.

The vibrissae are numerous; those above are black, the others white, and the longest extends a bit beyond the tip of the ear, which is $\frac{11}{12}$ inches (2½ centimeters) from the tip of the other ear.

It [the ear] is $\frac{9}{12}$ inches (2 centimeters) long; $\frac{5}{12}$ inches (11 millimeters) wide, round, and has short hair on the inside surface, chiefly at the posterior edge, which is appreciably longer than the anterior [edge].

The eye is a bit protruding; the teeth [incisors] are of an orange color, and the lower jaw is arguably somewhat protruding.

There are 4 digits on the front foot. The external one arises a bit more posterior than the internal one, and is shorter by $\frac{1}{12}$ inches (2 millimeters). The middle two originate a bit anteriorly, and are $\frac{1}{24}$ inches (1 millimeter) longer than the internal digit, and have very curved small claws. In addition, it has a thumb that originates a bit more posteriorly than the other digits, but it is so much shorter, that it is only upon careful examination that one perceives its claw.

The hind foot has five digits: the external and internal digits arise in parallel, but the internal one is longer and stouter. The others originate parallel to the [distal] tip of the inner digit, and they are equal [in size] to each other. The tarsus is $\frac{14}{12}$ inches (3 centimeters) long, including the claws, hairy and olive-hued, like the sole of the fore-foot.

The two specimens are female, and their vulva bear resemblance to that of the female spiny rat; but it seems to me that the largest has not borne young.

From the muzzle to the tail, and on the sides of the body, all is cinnamon-brown, because the hairs have a small cinnamon tip; then they become darker and finally white near the skin. All of the underparts of the animal are whitish, lighter under the head, and darker between the front legs; the pelage is soft, very dense, and the fur at the base of the ear, conceals the opening of the ear [external auditory canal].

Before 1959, when Hershkovitz pointed out that Olfers' (1818) *buccinatus* was an older name than Desmarest's (1819) *angouya*, most authors through the decades applied Desmarest's name to animals they thought fit Azara's description, which resulted in descriptions of apparently different

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[13] Darton and Clark (1994: 244), in their survey of measurement, related that a league is a

> measure of distance generally used only in poetic or romantic contexts, and accordingly varying in value in different countries. In English-speaking countries, however, the league is reckoned to equal 3 miles—but even these miles are not the same in the United Kingdom and the United States, and in the United Kingdom they are not the same on land and at sea . . . . Elsewhere in the world, where the UK terrestrial unit has not been adopted, the unit has been standardized within the metric system of measurement (as exemplified in France). 1 French league (*lieue*) = 4 kilometres.

We used 3 statute miles or 4.828 km (the U.K. league on land) to estimate the distance indicated by Azara's leagues. Modern Atyrá, presumably in the vicinity of Azara's ''Atira'' is located at 25°15′S/57°10′W in Departamento de La Cordillera (USBGN Paraguay, 1992: 4).

kinds of rats. Rengger (1830: 229), Wagner (1843: 534),[14] and Burmeister (1854: 168) provided the earliest accounts of any substance and described a rodent with reddish brown upperparts diffused suffused with an admixture of darker hairs, white underparts, and a brown tail slightly longer than length of head and body. Values for length of head and body and length of tail given by each author are: 135 and 147 mm (Rengger), 125 and 135 mm (Wagner), and 130 and 150 mm (Burmeister) (approximate conversions to millimeters from zolls and linie). Rengger noted that the ''mouse was found in thick undergrowth of a stony hill, where it lives in underground trackways.'' Larger individuals are older, wrote Wagner, more ''handsomely colored,'' and seemed to him to be basically like *Hesperomys leucogaster*. For Burmeister, ''the mouse, which must carry the name established by Azara, should be distributed over the greater part of inner Brazil, as it is not particularly scarce.''

In his report on the mammals collected on the ''Roosevelt Brazilian Expedition,'' Allen (1916b: 570) recorded a specimen captured at Trinidad, Paraguay, as ''*Oryzomys angouya* Desmarest.'' The stuffed skin and associated skull is in the collection at the American Museum (AMNH 36513). It has a large body with brownish tawny dorsal fur and whitish gray underparts and a long tail (lengths of head and body, tail, and hind foot as recorded on the skin label are 190, 190, and 40 mm, respectively). The specimen is an example of the large-bodied, long-tailed Brazilian forest rat currently known as *O. ratticeps*.

Sixteen years later, Gyldenstolpe (1932: 24) also recognized ''*Oryzomys angouya* Desmarest.'' He provided no measurements, only this description: ''General colouration above strongly grizzled with ochraceous buff and black, becoming clearer buff on the sides of the body. Ventral surface soiled greyish white with a pale buff wash, the hairs slaty at their bases.'' This general characterization could apply to at least three species of *Oryzomys* known to occur in Paraguay.

While Allen (1915) identified a large-bodied, long-tailed rat as *O. angouya*, Vieira (1953: 137), who discussed the rodents and lagomorphs of Estado do São Paulo, had a different view of Azara's species. He assigned three specimens to ''*Oryzomys angouya* (Desmarest),'' recording the measurements of one: length of head and body, 140 mm; length of tail, 120; length of hind foot, 30; greatest length of skull, 32 mm; and length of upper molar row, 5 mm. If these values were taken from an adult, they are close to those we obtained from series of *O. laticeps* (see table 4), which contrasts with *O. ratticeps* by being smaller in body size and having a tail either equal to or shorter than length of head and body.

After 1959, Desmarest's (1819) *angouya* was treated as a synonym of Olfers' (1818) *buccinatus*, but the change in name did not clarify identity of the species. In that year, Hershkovitz brought to the attention of taxonomist the work on Neotropical mammals by Ignatz von Olfers, and pointed out that Olfers (1818: 209) had proposed *Mus buccinatus* for Azara's (1801) ''Rat troisième, ou Rat Angouya'' (an arrangement Hershkovitz, 1955: 660, had previously indicated in a parenthetical notation). As synonyms of *Oryzomys buccinatus*, Hershkovitz listed *Mus angouya* Desmarest (1819: 62), *Mus Anguya* Rengger (1830: 229), *Hesperomys leucogaster* Wagner (1845: 147), *Hesperomys ratticeps* Hensel (1872: 36), *Calomys rex* Winge

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[14] In the collection at the Zoologische Staatssammlung München, there is a mounted specimen of an adult (skull is missing) identified by a brown label as ''*Originalexemplar zu Hesperomys Anguya* Desm. *in* Schreber-Wagner die Säugetiere 1843 Suppl. Bd. III S. 534.'' Another small label associated with the mount contains these notations: ''*Mus physodes* Licht/g2/B2/Brasil; *Hesperomys anguya* Desm./Brasilien Brandt; and *Hesperomys* [*Holochilus*] Anguya Desm./1842. Bras.''; this last notation is in Wagner's handwriting; the specimen is regarded as one of Wagner's types (R. Kraft, personal commun., letter in AMNH Mammalogy Archives). Alfred Gardner examined the mount in 1978. It has reddish brown upperparts that are paler along the sides of head and body, and nearly completely white underparts—the hairs have long white tips that mask the basal gray portion. Gardner identified it as *Oryzomys nitidus*, which was the name at that time applied to examples of Brazilian *O. russatus*.

This specimen is not a type. Wagner (1943: 543) simply identified it as a specimen of Desmarest's *Mus angouya* and used it for his account of ''25. H. Anguya Desm. Die Anguyamaus.''

(1887: 50), *Oryzomys ratticeps tropicius* Thomas (1924: 143), and *Oryzomys ratticeps paraganus* Thomas (1924: 143). Hershkovitz unhesitatingly allied Azara's ''Rat Angouya'' with what had been cited in the professional literature for more than eight decades as *O. ratticeps*, stating that ''Azara's description of the *angouya* leaves no doubt of its identity with the species of *Oryzomys* subsequently described under the several names listed in the above synonymy.''[15]

Ávila-Pires (1960), reporting on his concept of the *Oryzomys ratticeps* group, recognized three species: *O. ratticeps* and *O. leucogaster* from southeastern Brazil, and *O. buccinatus* from Paraguay. He pointed out that the original descriptions were not sufficiently detailed to support the synonymy of *ratticeps* with *buccinatus*. Ávila-Pires' definition of *buccinatus* was basically similar to Azara's (1801) description of the ''Rat troisième, ou Rat Angouya.''

Cabrera (1961: 384), in his catalog of South American mammals, recognized *O. buccinatus* as a separate species and under it listed the citations to *angouya* by Desmarest (1819), Rengger (1830), Wagner (1843), Burmeister (1854), Trouessart (1898), and Allen (1916b). Cabrera gave Paraguay and northern Argentina as the range of *O. buccinatus*, but provided no indication why he considered it something different from other species of *Oryzomys*. He also recognized *O. ratticeps* (p. 395) as a species separate from *O. buccinatus*.

Unlike Cabrera, Myers (1982) did specify an identity for *O. buccinatus* and in doing so differed with Hershkovitz's definition and provided yet another species to which Azara's description might apply. Reporting on the ''Origins and affinities of the mammal fauna of Paraguay,'' Myers used the name *Oryzomys buccinatus* for a species occurring only in the region east of the Paraguay River, noting that it ''closely resembles or is identical with *Oryzomys subflavus*, a species of forests and forest edges in southeastern Brazil'' (p. 89). Earlier, Cabrera (1961: 396) had listed *O. subflavus* as a distinct species found in ''Brasil oriental.'' Hershkovitz omitted *subflavus* in his list of synonyms for *O. buccinatus*, and published evidence indicates that he considered *subflavus* to be a separate species (see Hershkovitz, 1960).

We will never know the actual species on which Azara based his description of the ''Rat Angouya.'' The animals he had in front of him had ''cinnamon-brown'' upperparts from the ''muzzle to the tail, and on the sides of the body,'' whitish underparts (''lighter under the head, and darker between the front legs''), and soft, dense pelage. Lengths of head and body, tail, hind foot, and ear recorded by Azara are 150, 160, 30, and 20 mm, respectively. If this combination reflects adult traits, Azara could have been describing what we call *Oryzomys nitidus*, which occurs in eastern Paraguay, but is apparently uncommon (see localities 145 and 146 in gazetteer for *O. nitidus*). The chromatic and dimensional traits noted by Azara are more like *O. nitidus* than any other Paraguayan sigmodontine. However, the fur color and external dimensions also resemble young adult *O. subflavus* or even very young adult or juvenile *O. ratticeps*, two species that are found in eastern Paraguay and appear to be more common than *O. nitidus*. Examples of *O. subflavus* have longer tails (table 37), and most *O. ratticeps* have larger bodies, longer tails, and bigger hind feet than do Azara's animals (table 51). Philip Myers (personal commun.) suggested that Azara's description could also apply to *Oecomys mamorae*, which is native to Bolivia and Paraguay. External measurements of this *Oecomys* are close to the values recorded by Azara (lengths of head and body, tail, hind foot, and ear from four specimens collected in Paraguay are 143–151, 161–182, 26—30, and

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[15] Hershkovitz (1959: 348) also claimed Brants (1827: 141) ''had already determined as an *angouya* the specimen in the Vienna Museum later described by Wagner as *leucogaster*.'' Brant wrote ''Met deze soort voegt Desmarest den *M. brasiliensis* Geoffr. tezamen, daar wy laatsgenoemde niet gezien hebben, kunnen wy niets met zekerheid hierover zeggen, dan dat my deze soort toeschynt onder den naam van *M. leucogaster* in het K. K. Brasiliansche Museum te Weenen te berusten.'' Our translation (made by E. Brothers) of this paragraph does not support Hershkovitz's assertion: ''Desmarest combined this species with *M. brasiliensis* Geoffroy, but because we have not seen the latter, we cannot comment with certainty whether my *angouya* is housed under the name *M. leucogaster* in the K. K. Brazilian Museum in Vienna.''

20–22 mm, respectively), but its upperparts are gray with a slight tawny suffusion and have buffy strips along sides of the head and body.

Although Myers entertained such candidates as *Oecomys*, he has usually argued that Azara's description of the ''Rat troisième, ou Rat Angouya'' fits best with the species we recognize in this paper as *Oryzomys subflavus* (Myers, personal commun.). Recently he wrote us that his argument is based on Azara's measurements (personal commun., March 1, 1997, in AMNH Mammalogy Archives; our insertions are in brackets):

> First, consider the [hind foot] measurements. The only way I can make any sense out of them is by assuming that Azara measured on the dorsal surface of the hind foot. That way [*Oryzomys*] *megacephalus* [described by Azara as ''Rat-second, ou Rat à grosse tête,'' see our account of that species], for example, comes out about right, and the measurement he gives for Angouya is consistent with either [*Oryzomys*] *subflavus* or what I called [*O.*] *ratticeps*. [*Oryzomys*] *nitidus* . . . and [*Oecomys*] *mamorae* then are too small to be in the running for Angouya. That's pleasing because they [are] rare . . . and I think unlikely to be the correct choice on that basis also [assuming population densities at the time Azara worked were similar to what they are at present, which is arguable for *O. nitidus*].
>
> Next, consider Azara's body and tail measurements. The only way they can be right for either [*O.*] *subflavus* or [*O.*] *ratticeps* is if the animal is juvenile. I went to our collection [UMMZ]. We have a juvenile [*O.*] *ratticeps* that is a little smaller but not a bad match (291-142-33-24) [in mm; comparable measurements for total length, and lengths of tail, hind foot, and ear that were given by Azara are 310-160-30-20 mm, respectively]. The pelage over most of the back is distinctively gray—apparently, [*O.*] *ratticeps* is one of those *Oryzomys* with juvenile pelage rather different from adult. It doesn't fit Azara's description of the pelage of the Angouya at all [Azara described the upperparts as ''cinnamon-brown'' and the underparts as whitish]. I then found a young [*O.*] *subflavus* (283-152-37-20). The juvenile pelage is slightly grayer than adult and the fur is slightly woollier, but Azara's description is acceptable. So I thought I had shown that if you look at animals the same size as Azara's, they are in fact distinct and *angouya* = *subflavus*. But it of course isn't quite that simple. In poking around today, I found another young [*O.*] *ratticeps*. This one is a little larger than Azara's (322-169-35-23). It has adult pelage. So it looks like the juvenile/adult molt takes place at about the body size of the animal that Azara described, and it seems possible that he had a 310 mm [*O.*] *ratticeps* with adult pelage.

So at least three species of Paraguayan *Oryzomys* can be associated with Azara's description. Had Hershkovitz (1959) not linked *O. ratticeps* with Azara's ''Rat Angouya,'' we could have associated Azara's description with *O. nitidus* (to us, Azara's ''cinnamon-brown'' upperparts and whitish underparts are most like *O. nitidus*), designated a neotype, and replaced the name *nitidus* with *angouya*. Others might argue, as P. Myers originally did, that *angouya* should replace *O. subflavus* because Azara's description generally fits that species (not as well as *nitidus*, however) and has been collected more frequently than *nitidus*, suggesting it is more common. Either action would stabilize the name *angouya* but eliminate names that are familiar and have been used extensively in the literature (a plethora of publications documenting ecological and distributional results for Brazilian rodents include samples identified as *O. subflavus*). Another option would be to consider the species Azara described as unidentifiable and interpret the scientific names based on his account as *nomen dubia* (*angouya* and *buccinatus*); in this case, the meaning and utility of *nitidus* and *subflavus* would not be jeopardized, and Wagner's (1845) *leucogaster* would be the oldest name available to replace Hensel's (1872) *ratticeps*.

However, Hershkovitz (1959: 347–348) has formally associated Azara's ''Rat troisième, ou Rat Angouya'' with Hensel's *ratticeps* through Olfers' *buccinatus* and Wagner's *leucogaster*. We accept Hershkovitz's synonymy, even though the traits of *O. ratticeps* seem the most unlike those enumerated by Azara as compared to the characteristics of *O. nitidus* and *O. subflavus*, and we also relegate Olfers' (1818) *buccinatus* and Desmarest's (1819) *angouya* to synonyms of Fischer's (1814: 71) *Mus angouya*: ''4. *M. angouya* d'Azara, l. c. p. 86 (p. 71).'' Fischer's work is ''available'' in the sense of article 12a of the *International Code of Zoological Nomenclature* (1985 edition), a conclusion we defended previously in our account of *O. megacephalus*. Hershkovitz (1987: 62), in an exposition of mammals described by Azara and the current scientific names connected with them, also listed *Oryzomys angouya* Fischer (1814) as the name for Azara's ''Rat Angouya,'' noting that it ''antedates *Oryzomys buccinatus* Olfers.''

The next logical procedure is to designate and describe a neotype for *Mus angouya* Fischer (1814). We take this action to promote nomenclatural stability in a broad sense because it forever links the scientific name *angouya* to an actual example of a diagnosable species occurring in Paraguay and it preserves the names *nitidus* and *subflavus* by preventing designation of a neotype for *Mus angouya* by using an example of either of these two species (something we had not considered until R. S. Voss mentioned the possibility). Following our description of the neotype, we discuss identities of specimens on which each synonym of *Oryzomys angouya* is based, and explain why the samples do not represent any species in the former *Oryzomys* ‘‘*capito*’’ complex.

DESIGNATION OF NEOTYPE FOR *ANGOUYA*: Myers (1982: 90) noted that *Oryzomys ratticeps*, a species of the forest, is ‘‘common in eastern Paraguay’’ and also ‘‘known from dense but typically Chacoan forest at a single locality in the lower Chaco.’’ Azara’s specimens of the ‘‘Rat Angouya’’ he described were brought to him from ‘‘the slope of a mountain gorge inhabited by the tribe of Atira’’ (see translation of Azara’s description). Modern Atyrá is in the Departamento de La Cordillera at 25°15′S/57°10′W (USBGN Paraguay, 1992: 4). During his survey in Paraguay, P. Myers (personal commun., letter in AMNH Mammalogy Archives) did not obtain *ratticeps* from the Atyrá region, but did obtain ‘‘a dozen or so’’ in Departamento de Las Misiones near San Antonio where, Myers recalled, ‘‘the vegetation is more or less like what is found at Atyrá, today at least.’’ He also noted that compared with Atyrá, San Antonio is much less rocky and hilly. From this series, P. Myers sent us UMMZ 124201, a young adult male captured by him (collector’s number, 2253) at 2.7 km (by road) N San Antonio (locality 6 on the map in Myers and Carleton, 1981: 2) on August 22, 1976. We designate this specimen (UMMZ 124201) as neotype for *Mus angouya* Fischer (1814: 71), the oldest name (to our knowledge) available for Azara’s (1801: 86) ‘‘Rat troisième, ou Rat Angouya.’’

The neotype consists of a museum study skin (fig. 145), cranium and mandible (figs. 146, 147), intact dentition (fig. 148), and carcass preserved in fluid (originally fixed in a formalin solution and later transferred to a mixture of ethanol and water). The skin and skull are in excellent condition; accessory glands were partially dissected on the carcass (one of the specimens surveyed by Voss and Linzey [1981: 40] in their comparative study of male accessory glands among Neotropical muroids). External, cranial, and dental measurements are listed in table 51.

The neotype is a large-bodied rat with a tail longer than head and body (table 51). Fur covering the dorsum is soft, moderately long (overhairs reach 10–12 mm on the back near the rump), and tawny brown. The middorsal region from head to rump is darker, and the sides are brighter; the face has a tawny gray tone. In addition to the dark brown eyelid, each eye is surrounded by a wide brown ring that contrasts with the surrounding fur. Ears are round, brown, and densely covered, inside and out, with short and fine brown hairs. Mystacial vibrissae are moderately long; when laid against the stuffed skin, the longest extend 10–15 mm beyond the ears. Underparts are buffy except for a whitish area on the throat; the venter coloration extends onto sides of the face to bases of the mystacial vibrissae. The long and finely haired tail is brown on all surfaces and terminates in a short tuft of hairs (5 mm long). Dorsal surfaces of front and hind feet are brownish gray, the digits are densely covered with silvery hairs, and dense ungual tufts nearly conceal the claws and extend appreciably beyond their tips. Plantar surfaces are brown and adorned with an elongate thenar pad and large hypothenar and interdigital pads. Each hind foot is long and wide. The three central digits are the longest, the first digit is very short, extending just beyond bases of the three center digits, and the fifth digit is longer, reaching about a third of the way along the central digits. Contrasted with the hind foot of *O. megacephalus* illustrated in figure 17, the foot of the neotype is wider relative to its length, and the two outer digits are longer relative to lengths of the inner digits.

The cranium is elongate in shape and robust in build. As seen from dorsal perspective, the rostrum is moderately long, the zygomatic notches are deep, the interorbit is narrow and defined by smooth (but angled,

Fig. 145. Stuffed skins of types. Dorsal and ventral views of the neotype of *Mus angouya* Fischer (UMMZ 124201) are on the left, the lectotype of *Hesperomys leucogaster* Wagner (NMW 450) is on the right. Measurements are listed in table 51.

not rounded) dorsolateral margins, the braincase is squarish, and the occiput is deep (anterior–posterior). In ventral view, the incisive foramina are long and narrow, terminating posteriorly beyond the anterior margins of first molars. The bony palate is short, its posterior margin about even with back faces of the third molars; prominent palatal pits adorn the posterolateral margins. Moderately large sphenopalatine vacuities border the presphenoid; otherwise, the roof of the mesopterygoid fossa is completely ossified posterior to the presphenoid. The moderately recessed pterygoid fossae and the anterior two-thirds of each pterygoid plate is solid except for scattered and minute perforations. The auditory bullae are small relative to size of the cranium, and each bony eustachian tube is long. In side view, the zygomatic plate is wide, each alisphenoid region lacks a strut (as a result, the masticatory–buccinator foramen and foramen ovale accessorius are coalesced), and a prominent hamular process separates a spacious postglenoid foramen from an enlarged subsquamosal fenestra. The tegmen tympani of the periotic does not reach the squamosal, a configuration similar to that in *O. palustris* (see Voss, 1993: 19). The neotype lacks a sphenofrontal foramen and squamosoalisphenoid groove and has a minute stapedial foramen, a diagonal groove in the dorsal surface of the pterygoid plate, as well as a tunnel-like medial entrance to the alisphenoid canal; these are all osteological landmarks of a derived cephalic arterial circulation like that found in *O. subflavus* and diagramed for *O. palustris* by Carleton and Musser (1989: 38). In this pattern, the stapedial artery has lost its three primary branches (stapedial, supraorbital, and infraorbital), and the supply to the orbit and upper jaw is taken over by a secondary connection to the internal carotid. ‘‘The secondary connection to the orbital–maxillary circulation,’’ as Carleton and Musser (1989: 35) described it, ‘‘branches from the internal carotid artery after the latter passes through the carotid canal. This branch next crosses diagonally over the dorsal surface of the pterygoid plate to enter the anterior end of the short alisphenoid canal and finally exits the braincase through the anterior alar fissure.’’

Each dentary is stocky with a deep ascending ramus, a small coronoid process, shallow sigmoid notch, and concave margin between condyloid and angular processes.

Enamel layers of incisors are pigmented: uppers are orange, lowers yellowish orange. The uppers emerge from the premaxillaries and curve back (opisthodont in configuration relative to rostral axis). Molars are brachydont. Their occlusal patterns resemble those typical of species in the *O. nitidus* group, and not the patterns common to *O. megacephalus*, *O. bolivaris*, and *O. talamancae* (see figs. 29–32, 151). Each second upper molar has a short paraflexus, an elongate medial fossette (enamel island), and a small labial fossette. In each second lower molar, the hypoflexid extends only to the middle of the tooth, the entoflexid (the fold opposite the hypoflexid) is short, and a large fossettid is present.

San Antonio is in the ‘‘Ecoregión Ñeembucu,’’ described by Acevedo et al. (1990: 30–31) as the ‘‘grandes zonas anegadizas e inundadas a consecuencia de sus características topográficas y el desborde de las aguas de los ríos Paraguay y Paraná. El rango altitudinal varía entre los 48 metros en las cercanías de Gral. Díaz y los 333 metros en el Cerro Yariguá.’’ The region includes a diverse range of ecological formations, according to Acevedo et al.: ‘‘Bañados, Esteros con Vegetación Herbácea y Arbustiva, Embalsados, Bosques en Suelos Saturados, Bosques en Suelos Inundados, Rios, Arroyos, Nacientes de Agua, Bosques Semicaducifolios Medios y Bajos y Sabanas.’’

ALLOCATION OF *BUCCINATUS* AND THE OTHER *ANGOUYA*: *Mus buccinatus* Olfers (1818: 209) and *Mus angouya* Desmarest (1819: 62) are scientific names based, in Hershkovitz’s (1959: 347) words, ‘‘solely on Azara’s *rat angouya*.’’ Rengger’s (1830) *Mus Anguya* is simply a misspelling also founded on Azara’s description.

ALLOCATION OF *LEUCOGASTER*: Pelzeln (1883: 67) credited Natterer for the name *leucogaster*, but the taxon was first diagnosed by Wagner (1845: 147) as ‘‘*Hesperomys leucogaster* Natt.’’ and credit for the name goes to him. Wagner’s original diagnosis is short: ‘‘H. supra fulvus, nigro-adspersus, subtus cano-lutescens; auriculis majusculis, pedibus fuscentibus; cauda corpore longiore, nuda; statura grandiore. Körper 6″ 10‴, Schwanz 7″ 9‴. Aus Brasilien.''

Three years later, Wagner (1848: 306–307) provided a fuller description of *leucogaster* in a section of species accounts under *Hesperomys* that Wagner designated ''a) *tawny pelage, tail much longer than body*'' (translated by E. Brothers; the German version is provided in appendix W):

> 1. *Hesperomys leucogaster* Natterer.
> The light-bellied Scharrmaus.
>
> Tawny above, sprinkled with black, grayish white below; ear somewhat larger, feet brownish yellow, naked tail longer than body. [from the Latin]
> *Hesperomys leucogaster*. A. Wagner in Archiv für Naturgeschichte 1845. p. 147.
>
> This Scharrmaus is similar to *Hesperomys subflavus*, but is larger, the tail much longer, the coloring livelier red, and the feet brownish. The ears are large, oval, broad and haired in a similar manner to *Hesperomys Anguya*; the front thumb is very small and bears a truncated nail; the tail is much longer than the body, naked, scaled, and with only a few small hairs visible among the scales. The upper side is colored as in *Hesperomys Anguya*, but with a little more red. The underside appears dirty yellowish gray because the hair is gray against the base and yellowish at the outer parts; the hairs of the throat, lower jaw, and the anal region are of one color, and uniformly paler as well. The color of the head is paler than that of the back, and grayish around the upper lip. The whiskers are black, the feet are covered with brownish hairs, the soles are naked and light-colored. The tail is brownish gray with some brownish hairs.

Body	6″	10‴	Ear	0″	10‴
Tail	7	9	Hind foot	1	6[9]

> In the forest of Ypanema (São Paulo); received through Natterer. On a female the mammae number 8: 2 between the forelimbs, 2 behind the forelimbs, 2 in front of the thighs, 2 between the thighs.

In 1854, Burmeister (pp. 170–171) provided his amplified description of ''*Hesperomys leucogaster* Natterer,'' which was included in a subsection of that genus labeled *Calomys* (translated by E. Brothers; transliteration of the German version is provided in appendix X):

> 6. Hesperomys leucogaster *Natterer*
> Abhand. d. Münch. Acad. phys. Cl. V. 306. 1.
>
> Reddish yellow-brown above, mixed with black-brown hairs; gray-white below, with a yellowish belly; tail longer than the body, practically naked; body 6⅔″, tail 7¾″.
>
> Fur rather thick, long and very soft to the touch, the entire upperside is of a reddish yellow-brown color; the forehead, around the eyes and the back, is purer brown; the snout is conspicuously grizzled, the nape of the neck and sides are more red-yellow, the cheeks and the ear region are grayish. From under the chin down to the anus is gray-white, the throat is pure white, the abdomen yellowish-tinged. All the hairs are slate-gray in the deep part, brown in the middle, the tips of most are red-brown, many more are light golden-yellow, a few are black-brown, these last are somewhat longer and stronger bristles. Upper lip flecked with a whitish color at the corners of the mouth; the sides near the throat and the chest between the forelimbs are grayish. The back color extends down the forelegs to the backs of the hands, becoming gradually duller; on the hind limbs, the front surface of the knee is white touched with gray overall; the instep is brownish and the toes, like those of the fore feet, are white; the naked soles of the hind legs are dark flesh colored, brownish. The long thin tail has very fine scales and a uniformly short, sparse brownish hair coat which forms a slight tuft at the tip. The long whiskers are brown, the lower ones are white, the tips of the longest reach out past the shoulder and are touched with a whitish tint. The ear is oval, not particularly wide, and covered with short brown hairs; those on the front edge are thicker and longer.
>
> Greatest length 14″; head and body 6¼–6½″; head, to the ear 1¼″; tail 7½–7¾″; hind foot 1½″; inside of the ear 7‴. From São João Rei.[9]
>
> Note 1. The specimen that Wagner wrote about was caught by Natterer at Ypanema in São Paulo; Brants thinks it is close to *Mus Anguya* (Muiz. 142), which I believe is the name ascribed to this species in the Berlin collection.
>
> 2. *Holochilus leucogaster* Brandt, 1. 1. 428 2. th. 12, has almost exactly the same body proportions and exactly the same markings, but appears in the illustration, which was made from life, to be a much lighter red-yellow, nearly as light as *H. physodes*. The description exaggerated the long whiskers so that they reach to the middle of the body. The hind foot should be 1″7‴ long and its sole is black.
>
> 3. Another species with equally long whiskers was distinguished by Dr. Lund as *M. mystacalis* Blik. p. Bras. Dyrev. III. Till. 279. The animal is 12″ long, of which 5″ is the body and 7″ comes from the tail; the color is reddish-gray above, whitish below; the tail ends in a more elongate tuft of hair. Both of the preceding species must be placed very close to [*H. leucogaster* Natterer].
>
> 4. The same authors (loc. cit.) are eager to include *Mus vulpinus* here; at least it approaches these other, very similar species, when it does not coincide at all, I suspect, with *H. leucogaster*. Its length is 12″ 6‴, of which 5″ 5‴ comes from the body, 7″ 1‴ from the tail; the fur is unusually long-haired, lively rust-red above, and white tinged with rust-yellow below.

The descriptions of Wagner and Burmeister clearly reflect the characteristics of large body size, very long tail, dark brown upperparts, and whitish gray or buffy gray underparts that are associated with the species in-

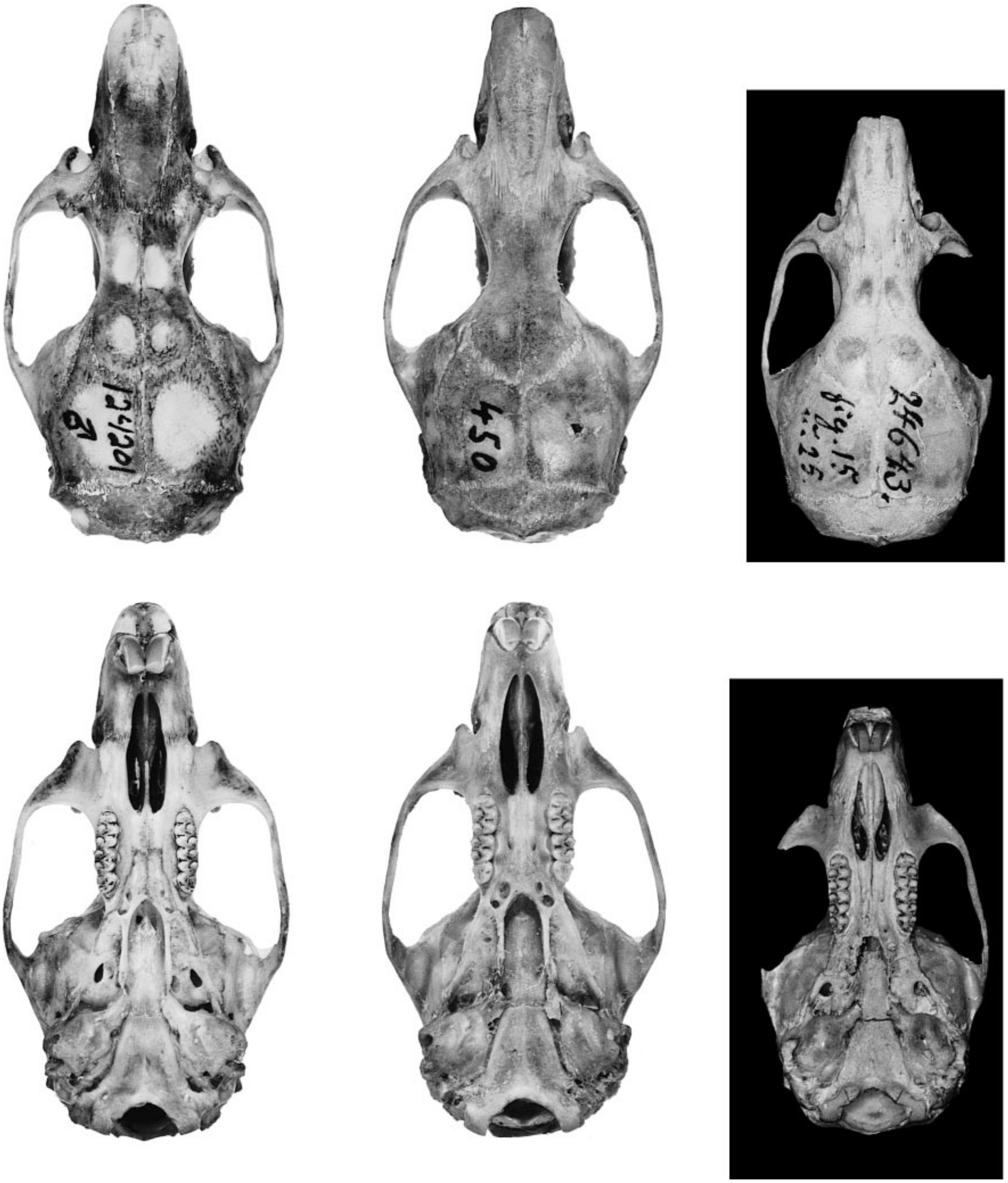

Fig. 146. Dorsal (**top row**) and ventral (**bottom row**) views of crania from types associated with *Oryzomys angouya*. **Left**, neotype of *Mus angouya* Fischer (UMMZ 124201, young adult male), near San Antonio, southeastern Paraguay; **middle**, lectotype of *Hesperomys leucogaster* Wagner (NMW 450, young adult female), Ipanema, Brazil; **right**, lectotype of *Hesperomys ratticeps* Hensel (ZMB 47721, juvenile–young adult female; number indicated on cranium is not the ZMB catalog number), Estado do Rio Grande do Sul, Brazil. ×2. Measurements are listed in table 51.

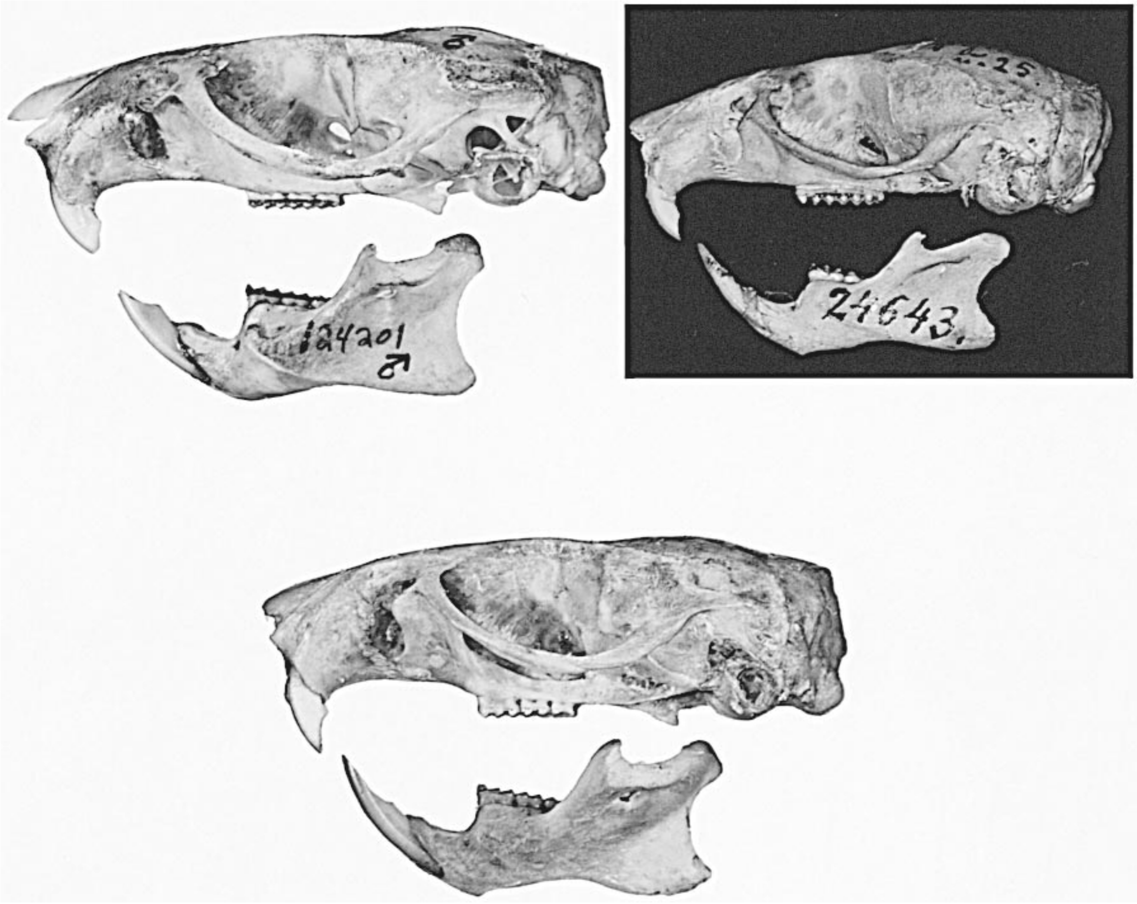

Fig. 147. Lateral views of crania and left dentaries of same types portrayed in figure 146. **Upper left,** Neotype of *Mus angouya*; **upper right**, lectotype of *Hesperomys ratticeps* (number shown is not the ZMB catalog number); **lower center**, lectotype of *Hesperomys leucogaster*. ×2.

cluded in current checklists as *O. ratticeps* (Musser and Carleton, 1993: 724).

Wagner did not designate a holotype for *Hesperomys leucogaster* or indicate the number of specimens he used. The pelage traits and dimensions listed are clearly from an adult, and he does refer to the mammae count on a female, which we presume to have been adult as well. In his report on the Brazilian specimens collected by Natterer, Pelzeln (1883: 67) identified four specimens collected at Ipanema (all under Natterer's field number 75) as *Hesperomys leucogaster*. Only three can be located in the collection at Wien. When G. G. Musser visited there, he found only the skulls of two young adults, NMW B448 (captured June 11, 1820) and B450 (captured June 14, 1821). Subsequently, Barbara Herzig found the skins for those two specimens and an additional skin only (NMW B449, captured January 3, 1822) representing an adult. All three exhibit the traits associated with what has been known as *Oryzomys ratticeps* (figs. 142–144) as well as with the neotype of *O. angouya* (figs. 146–148; see description of the latter). We regard NMW B448, B449, and B450 to be syntypes. Of the three specimens, NMW B450 is the most complete (NMW B449 is a skin only and the cranium of NMW B448 has a damaged rostrum and basicranial region).

We designate NMW 450 lectotype for *Hesperomys leucogaster* Wagner (1845: 147)

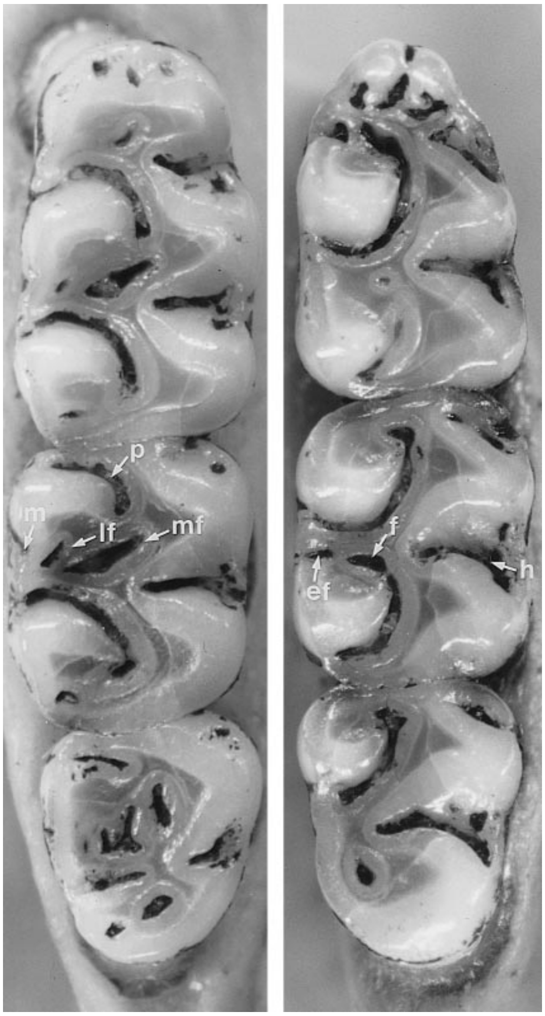

Fig. 148. Occlusal views of right upper and lower molar rows from the neotype (UMMZ 124201) of *Mus angouya* Fischer. Abbreviations: **ef**, entoflexid; **f**, fossettid; **h**, hypoflexid; **lf**, labial fossette; **m**, mesoflexus; **mf**, medial fossette; **p**, paraflexus.

following the guideline in recommendation 73F (p. 151) in the *International Code of Zoological Nomenclature* (1985 edition). This example is a young adult female obtained at Ipanema (''Ypanema'' is the spelling on specimen labels; 23°26′S/47°36′W), Estado do São Paulo, Brazil, by J. Natterer on June 14, 1821. Measurements are listed in table 51. The stuffed skin is intact, but in fragile condition (fig. 145) and the skull is complete (figs. 146, 147). This may well have been the specimen described by Wagner in 1848 because the specimen fits his description, particularly the measurements, which Wagner recorded in the German zoll (two apostrophes), which is roughly an inch, and linie (three apostrophes), about $^{1}/_{12}$ of an inch (see footnote 9). Wagner's values, their approximate equivalent in inches, and our values in inches, respectively, derived from Musser's measurements of the skin (performed before he converted Wagner's units to inches) are: length of body, 6″ and 10‴ = 6 and $^{10}/_{12}$ in. = 6¾ in.; tail, 7″ and 9‴ = 7¾ in = 7¾ in.; hind foot, 1″ and 6‴ = 1½ in = 1½ in.; ear, 0″ and 10‴ = $^{10}/_{12}$ in. = ¾ in. (Musser also recorded the measurements in millimeters, and these are listed in table 51). Mammae are conspicuous on the preserved skin.

With a few exceptions (Fitzinger, 1867: 90; Tate, 1932b: 2; Hershkovitz, 1959: 347; Ávila-Pires, 1960: 6), Wagner's *Hesperomys leucogaster* has been ignored in the literature. Ávila-Pires (1960: 6) recognized *Oryzomys leucogaster* as a separate species, noting that collections in the Museo Nacional at Rio de Janeiro contain a series from Anápolis in Estado de Goiás exhibiting traits fitting Wagner's description. We have not seen that series, but specimens in the American Museum of Natural History collected at Anápolis are examples of the taxon Thomas (1924) described as *O. lamia* (see our account of that population in the sections on *O. nitidus* and *O. russatus*). These are large-bodied rats with pelage coloration generally resembling Wagner's description of *leucogaster*, but in all other features they are strikingly unlike *O. ratticeps*, which to our knowledge, has not been encountered in the state of Goiás. Judged by our study of the type series of *leucogaster*, it is, as indicated by Hershkovitz (1959: 347), an older and available name for the same species to which *ratticeps* (Hensel, 1872: 36) has been applied. Brandt's (1835: 428) *Mus leucogaster* also is older, but applies to a different species (R. S. Voss, personal commun.).

ALLOCATION OF *RATTICEPS*: For more than a century, the name *ratticeps* has identified a large-bodied, long-tailed species of *Oryzomys* occurring in eastern Brazil and eastern Paraguay (Trouessart, 1898: 525, 1904: 420;

Thomas, 1924: 143; Gyldenstolpe, 1932: 13; Ellerman, 1941: 420; Musser and Carleton, 1993: 724). The only exception is Hershkovitz's (1959: 347) treatment of *ratticeps* as a junior synonym of *Oryzomys buccinatus* (Olfers, 1818: 209), the oldest name he considered applicable to this long-tailed *Oryzomys*.

Hesperomys ratticeps was described by Hensel in 1872 (pp. 36–37; translated by E. Brothers; the version in German is reproduced in appendix Y):

> 22) *Hesperomys ratticeps* n. sp. Fig. 15 u. 25
>
> In the upper jaw, the crest of the pillar at the front end of M1 has a shallow, median groove which divides it into two points; the smaller is clearly the tubercle of the tooth crown. At M3, the anterior double-tubercle is clearly divided; the posterior enamel line is reduced, its tubercle is barely suggested. Incisors, taken together at the cutting edge, are 2.40 mm wide.
>
> In the lower jaw m1 the front pillar clearly separates into two points and the groove itself is visible from the front side of the tooth; at m3 the posterior double protuberance is reduced and forms a truncated cone-shaped pillar with a fused cavity at the peak. At m2 and m3 a basal swelling arises in front of the outer tubercle of the anterior double protuberance, fashioning a narrow channel represented as a transverse, which in m1 separates the front pillar into the double protuberance.
>
> Upper molar tooth row 6.0 mm long; length of M1 2.60 mm, length of M2 1.80 mm, length of M3 1.50 mm. Lower molar tooth row 6.0 mm long; length of m1 2.45 mm, length of m2 1.90 mm, length of m3 1.85 mm.
>
> The nasals are as broad as the frontal process of the upper jaw. The width of the forehead between the eyes is somewhat smaller than the length of the upper molar tooth row. The interparietal is large, as in *Mus decumanus*. Supraorbital margin does not possess a sharp edge, but also is not rounded. Incisive foramina are close together behind the middle of the widest part; the ends are immediately anterior to the transverse line of the first molars and are somewhat pointed, but the fronts are truncated.
>
> Basicranial length of the largest skull (old female) is 31.0 mm. Nasals 14.4 mm. Incisive foramina 8.0 mm. Breadth of the forehead between the eyes is 5.0 mm. Breadth across the interparietal is 3.9 mm. Breadth across the frontals is 10.6 mm.
>
> The skeleton has 12 pairs of ribs, 7 unattached lumbar vertebrae, 3 sacral vertebrae, the third incompletely connected to the pelvis. 39 caudal vertebrae; the 17th vertebra is the diaphragmatic.
>
> The ears are large. In fresh specimens they extend to the front corner of the eye; in specimens preserved in spirits they do not reach the eyes. Upper lip is split. On the thumb of the hand there is a truncated fingernail. The sole of the tarsus is bare. The tubercle on the inner side of the sole is long and robust. The long tail is very finely and sparsely haired, and finely but distinctly scaly; the end possesses a faint hair tuft.
>
> The color is similar to *Mus decumanus*. The entire upper side is yellowish gray. The underfur hairs are mouse gray at the base, yellow (fawn-colored) at the tip; the whiskers are black. On the entire venter the underfur hairs are yellowish white, almost white at the throat. The outside of the ears are covered with fine hairs on the border. The tail is unicolor.
>
> For the largest specimen in spirits the head and body measure 155 mm, the tail 210 mm and the hind foot 34 mm.
>
> The animal was found only in virgin forest, where it was occasionally trapped in trees, but it also frequented provision stores of plantations.
>
> Collected were 2 skeletons, 1 skull, 6 large specimens and one fetus in spirits.

All of Hensel's material was collected in Estado do Rio Grande do Sul, Brazil, and is preserved in the collection of the Zoologisches Museum at Berlin. When A. L. Gardner worked there in 1978, he located seven specimens of *ratticeps* that formed the basis of Hensel's description (ZMB 47717–47722, 47730); all can be considered syntypes. Associated with ZMB 47721 was a label with the notation, ''Fig. 15/F. 25,'' which refers to Hensel's published drawings of molars from ''*Hesperomys ratticeps*'' (fig. 149). The specimen is a young female (figs. 146, 147; its cranium is marked with the numbers 24643 and B656). We designate it (ZMB 47721) lectotype for *Hesperomys ratticeps* Hensel (1872), following recommendation 73F (p. 151) in the *International Code of Zoological Nomenclature* (1985 edition).

ALLOCATION OF *REX*: Winge (1887: 50) described his new species, *Calomys rex*, from cave fragments collected by P. W. Lund from Lagoa Santa in Estado de Minas Gerais, Brazil (see locality 198 in gazetteer for *O. russatus*). The description is short (translated by S. Hoslett; the Danish version is reproduced in appendix Z):

> Only fossilized, but somewhat common, in caves of Lapa do Capão Secco, da Escrivania Nr. 3, Nr. 5 and Nr. 11, in a saltpeter cave by Escrivania, Lapa da Quebra Chavelha and da Serra das Abelhas.
>
> Known only from the anterior part of the skull.
>
> It is a tolerably unique (ad. individual) species; in the shape of the frontal it resembles somewhat *C. anoblepas*; it is larger than the other species of *Calomys*, about like *Nectomys squamipes*.
>
> From *C. laticeps* it deviates in the following:
>
> It is much larger.
>
> Skull. Moderately sharp crests from the labial muscles on the body of the maxillary ahead of the cheek

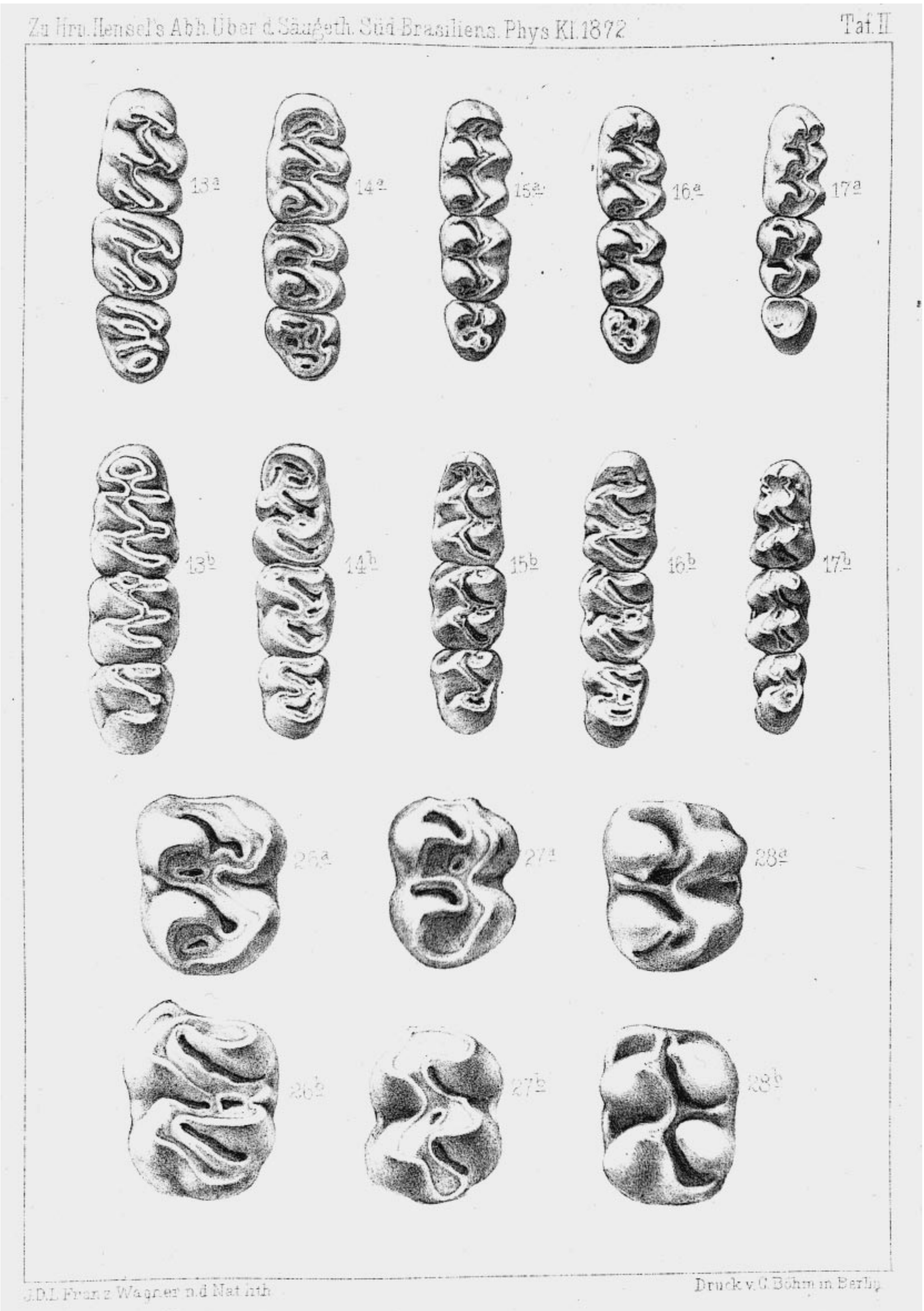

Fig. 149. Copy of Hensel's (1872) plate 2. Figures 15^a and 15^b portray upper and lower molar rows of ZMB 47721, the lectotype of *Hesperomys ratticeps* Hensel (1872).

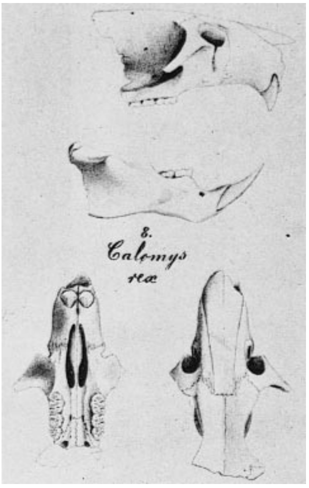

Fig. 150. Reproduction of Winge's (1887: pl. 3, fig. 8) illustration of *Calomys rex*.

> teeth. Frontal small, compressed, hollowed down lengthwise. No *Prc. supraorbitalis*: Orbital margin of the [interorbit] fairly sharp. The hard palate appears to extend quite far posteriorly.

Winge (1887: pl. III, fig. 8) illustrated an anterior portion of a cranium (intact except for missing zygomatic arches, from the end of the bony palate forward to tip of the nasals) from ''Lapa da Escrivania Nr. 5'' and a right dentary from Lapa da Serra das Abelhas. His measurements of the figured cranial fragment include length of ''upper molariform row, which was recorded as ''6½'' mm. Two other specimens from Lapa do Capo Sêco were noted to have upper molar rows of 6⅓ mm and 6½ mm, three examples from Lapa da Escrivania Nr. 5 range in length of upper molar row from 6½ mm to 6⅔ mm, and two fragments from Lapa da Serra des Abelhas measure 6¾ and 7 mm.

In justifying his synonymy of *rex* with *O. buccinatus*, Hershkovitz (1959: 348) noted that the ''original description, figures and measurements of the type [Winge did not designate a type. He illustrated a partial cranium that was collected in Lapa da Escrivania Nr. 5 and a dentary that came from Lapa da Serra das Abelhas; measurements were provided for both—see appendix Z.] agree in every detail with old adults of modern Paraguayan *buccinatus* in the collection of the Chicago Natural History Museum.'' Ávila-Pires (1959c: 27) documented two modern specimens of what he identified as *O. ratticeps* collected in the region of Lagoa Santa, and arranged Winge's *rex* as a synonym of *O. ratticeps*, which Hershkovitz (1959) treated as a synonym of *O. buccinatus*. We concur with these opinions. Winge's figure (reproduced in our fig. 150) of the cranial fragment closely resembles specimens of *O. ratticeps* of comparable age in the collection of the American Museum of Natural History, and his recorded value of ''6½'' mm for length of upper molar row of the cranial fragment is consistent with the range of values documented for *O. ratticeps* (table 51; Thomas, 1924; Ávila-Pires, 1960). We have not seen the actual specimens from which Winge's figure was drawn.

ALLOCATIONS OF *TROPICIUS* AND *PARAGANUS*: In 1924, Thomas (pp. 143–144) reported on the ''Geographical Races'' of *O. ratticeps* with this introduction: ''The fine coludo *Oryzomys ratticeps*, Hensel, ranges from São Paulo in the north to Rio Grande do Sul in the south, and westwards to Paraguay. A good series of it sent by Sr. E. Budin from Misiones has enabled me to compare its representatives at the three extremes of its range, and I find that they may be readily separated into three races. . . .'' Thomas then characterized *O. r. ratticeps* as ''Size smaller. General colour greyish brown, not markedly buffy as in the other forms. Skull about 39 mm. in greatest and 36–38 mm. in condylo-incisive length.'' The geographic distribution included the states of Rio Grande do Sul and Santa Catarina in southeastern Brazil and the province of Misiones in northeastern Argentina.

Thomas's next account diagnosed the new subspecies, *tropicius*, from the Brazilian states of São Paulo and Paraná in southeastern Brazil. In body size, *tropicius* was ''about as in true *ratticeps*,'' but differed by upperparts being ''buffy brown, the sides stronger buffy'' and underparts ''also more definitely buffy.'' Lengths of head and body, tail, and hind foot given by Thomas are 165, 205, and 35 mm, respectively; ''greatest length'' of skull, 39.5 mm, and ''upper molar series,'' 6 mm.

The third geographic variant, *paraganus*, was based on specimens from eastern Paraguay. Thomas diagnosed it as ‘‘Size decidedly larger than in the other subspecies, as gauged by the skull. Colour even richer and brighter than in *tropicius*, buffy brown, the sides clear buff. Under surface buffy whitish.’’ Impressed with the 15 specimens, Thomas explained that ‘‘This fine Paraguayan representative of *O. ratticeps* is readily recognizable by its greater size and brighter colour. Had it not been that one old specimen of subspecies *tropicius* has a skull as long as that of *paraganus*, one might have been tempted to consider the latter as a distinct species.’’ Lengths of head and body, tail, and hind foot, as provided by Thomas, are 197, 216, and 39 mm, respectively; ‘‘greatest length’’ of skull, 42.2 mm, and ‘‘upper molars,’’ 6.4 mm.

Thomas’s measurements of *tropicius* and *paraganus* point to a large-bodied, long-tailed *Oryzomys* with a large skull and long molar row. These are not characteristics of *O. russatus*. Furthermore, the crania (examined independently by G. G. Musser and A. L. Gardner) exhibit the qualitative traits associated with what is currently called *O. ratticeps* (figs. 142–144), including a derived cephalic arterial pattern.

REMARKS: *Oryzomys angouya*, as its morphological boundaries are currently understood, occurs in tropical and subtropical evergreen forests of eastern Brazil from the states of Minas Gerais (Ávila-Pires, 1959c), Espírito Santo and Rio de Janeiro (specimens in LACM identified by G. G. Musser), São Paulo and Paraná (Olmos, 1991; Thomas, 1924), and south to Rio Grande do Sul (Hensel, 1872; Ávila-Pires, 1994; Thomas, 1924). The distribution also ranges into northern Argentina in the provinces of Misiones (Massoia et al., 1987) and Jujuy (specimens sent by M. Mares to G. G. Musser for identification), and into eastern Paraguay (Myers, 1982).

In 1924, Thomas reported what he considered to be significant morphological variation among geographic samples of *Oryzomys angouya* (under the name *ratticeps*). The number of specimens now available for study certainly exceeds Thomas’s sample sizes, and the geographic range they represent is more expansive. A modern assessment of geographic variation in morphological and other characters among modern samples of this large-bodied, long-tailed rat is needed to determine whether the intersample variation reflects that within one species or represents a more complex taxonomic picture.

AFTERWORD

In 1964, Hooper and Musser presented a phyletic arrangement of Neotropical muroid species as inferred from morphology of the glans penis. There they recognized two subgroups within *Oryzomys*; *O. alfaroi* was placed in one assemblage of species, *O.* ‘‘*capito*’’ in the other. Hershkovitz (1966: 138) criticized this separation, complaining that it ‘‘highlights the inconsistencies between a classification based on a portion of a single organ, and one based on information from many sources, particularly a knowledge of variation within and between populations.’’ He continued (1966: 138) with an exposition of evolutionary relationships between the two species that brought into play other members of the *Oryzomys* ‘‘*capito*’’ complex as it had been defined by him in 1960:

> *O. capito* (or *talamancae*) and *O. alfaroi* can be distinguished by size and subtle cranial and dental characters where they are sympatric in Central America. In western Colombia and Ecuador the differences between *capito* and the smaller *alfaroi* become suspiciously narrow until in northern Peru *alfaroi* (now called *nitidus*) equals *capito* in all dimensions. Other differences remain tenuous or become insignificant. In the upper Amazonian region of tropical Ecuador and Peru, external, cranial and dental characters of the two evenly proportioned species persist in some populations, are recombined in others and in still others are randomly distributed without polarization toward one or the other phenotype. The same interplay of variabilities reappears in northeastern Brazil where the *alfaroi* type is known as *oniscus*. In southeastern Brazil the shifting roles of *capito* and *alfaroi* are enacted under the names *laticeps* and *intermedius*. Another nominal species, *Oryzomys lamia*, known from southern Brazil and Misiones, Argentina, enters as a third protagonist in this evolutionary interplay.
>
> The *capito-alfaroi* patterns of variation and dispersal indicate that divergence began in South Amer-

TABLE 52

Distribution of Some Distinguishing Features Among 11 Species in the Genus *Oryzomys*

	Species of *Oryzomys*								
Trait	*megacephalus*	*laticeps*	*tatei* *yunganus*	*bolivaris*	*talamancae*	*alfaroi*	*macconnelli*	*nitidus* *russatus*	*emmonsae*
Upperparts									
Bright tawny, ochraceous tones along sides of head and body					X		X	X	X
Darker, brownish tawny with burnished tones, only slightly brighter along sides of head and body	X	X	X	X		X			
Underparts									
Bright whitish gray to nearly solid white, cream highlights								X	X
Grayish white	X	X		X	X		X		
Dark gray slightly infused with white or pale buff			X			X			
Tail									
Bicolored, slightly mottled towards tip					X		X	X	X
Monocolored, ventral basal half often paler or mottled	X	X	X	X		X			
Front and hind feet									
Dorsal surfaces densely covered with white hairs, feet appear solid white					X		X	X	X
Dorsal surfaces sparsely covered with short silvery hairs, feet appear white or pale tan	X	X	X	X		X			
Ungual tufts									
Thick and silvery sheath, extending beyond claw tip	X	X			X	X	X	X	X
Tufts reach or extend beyond claw tips, but form sparser covering			X	X					
Superciliary, genal, and mystacial vibrissae									
Extend well beyond ears				X					
Reach pinnae but rarely extend beyond	X	X	X		X	X	X	X	X

TABLE 52
(*Continued*)

	Species of *Oryzomys*								
Trait	*megacephalus*	*laticeps*	*tatei yunganus*	*bolivaris*	*talamancae*	*alfaroi*	*macconnelli*	*nitidus russatus*	*emmonsae*
Alisphenoid strut									
Absent in 98–100% of sample	X	X	X	X	X	X	X		X
Present in about 50% of sample								X	
Sphenofrontal foramen and squamosoalisphenoid groove									
Absent	X	X	X						
Present				X	X	X	X	X	X
Parietal									
Extends below temporal ridge on side of braincase	X	X	X		X	X	X	X	X
Does not extend below temporal ridge				X					
Second upper and lower molars									
Labial and medial fossettes in M2, short hypoflexid in m2			X			X	X	X	X
Labial fossette only, elongate hypoflexid	X	X		X	X				

> ica, perhaps in the upper Amazonian valley. Invasion of Middle America by a population of either the "*alfaroi*" or "*capito*" chain provided conditions for speciation in isolation. Subsequent invasion of Middle America by representatives of the other chain completed a circular overlap with the ends of both chains most highly differentiated and completely isolated reproductively.

Unsubstantiated by documentation and without a foundation based on any taxonomic revision, these paragraphs portray a phylogenetic transcendentalism that perpetuated the mystery attached to the "evolutionary interplay" among members of the *Oryzomys* "*capito*" complex. In the years following 1966, members of this complex were regarded by researchers as difficult to identify and the species intractable to definition. Even if species limits could be described, associating correct scientific names with them seemed a Herculean task that darkened enthusiasm for the endeavor. The first glimmers of illumination came in 1976 with the publication of Gardner and Patton's report. In the present contribution we have tried to increase and broaden the spotlight with hypotheses of species limits for members of the former *O.* "*capito*" group that are grounded on primary sources—correctly identified specimens.

Unique distributions of qualitative traits, summarized in figure 151 and table 52, can be used to sort specimens of the former *Oryzomys* "*capito*" complex into definable entities. A modified cephalic arterial circulation (no sphenofrontal foramen or squamosoalisphenoid groove) combined with occlusal patterns of second upper and lower molars (long paraflexus and no medial fossette on the upper tooth, elongate hypoflexid on the lower) distinguish members of the *O. megacephalus* group (*O. megacephalus* and

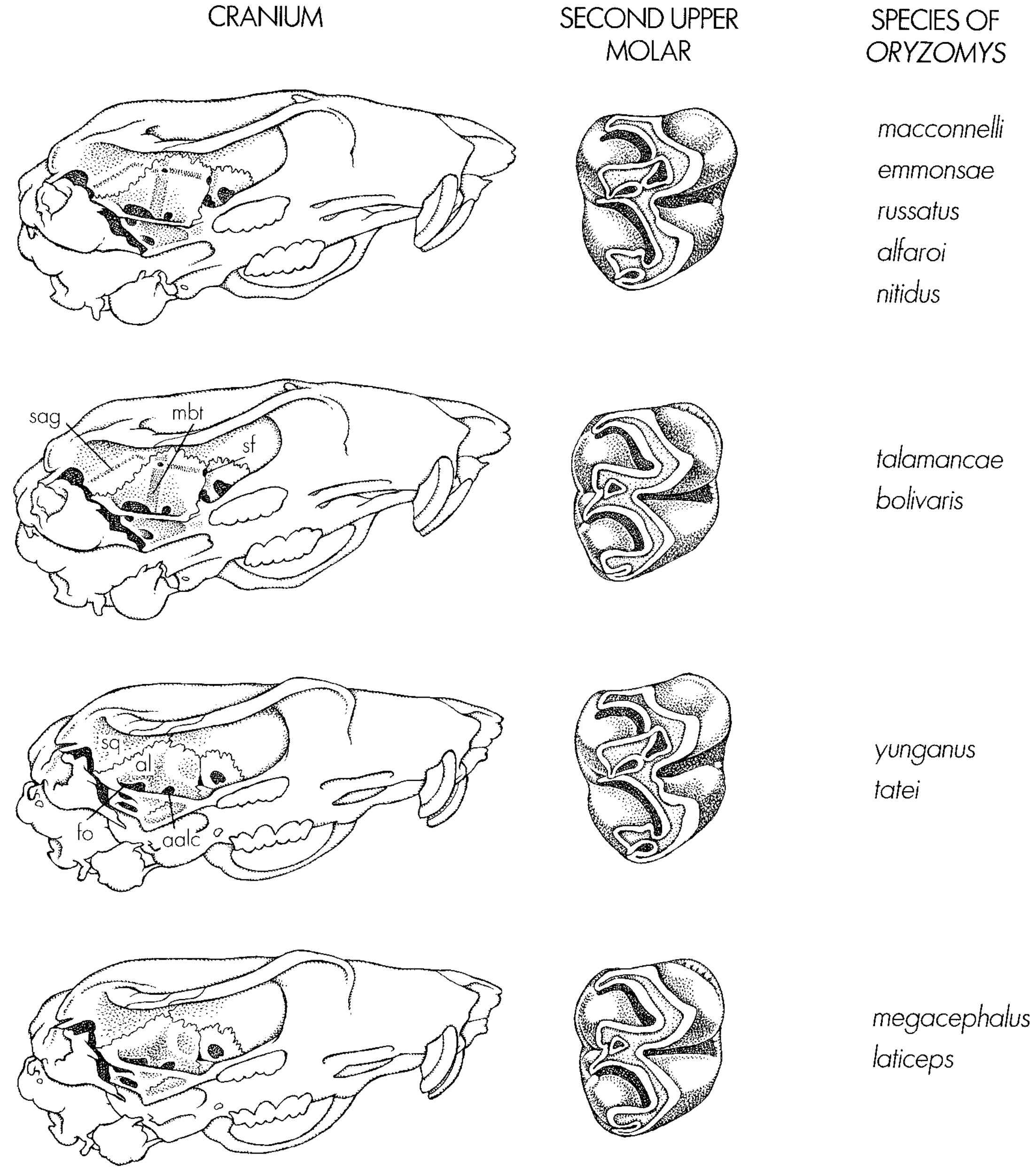

Fig. 151. Summary of variation in the carotid arterial circulation and occlusal pattern of the second upper molar in 11 species of *Oryzomys*. Cranial abbreviations: **aalc**, anterior opening of the alisphenoid canal; **al**, alisphenoid; **fo**, foramen ovale; **mbt**, trough for masticatory–buccinator branch of maxillary nerve; **sag**, squamosoalisphenoid groove on inside of braincase; **sf**, sphenofrontal foramen; **sq**, squamosal. All specimens of each species have a large stapedial artery and groove on the ventral surface of the pterygoid plate in which the infraorbital branch of the stapedial courses; these bony landmarks are illustrated in figure 27. The same molar drawings are portrayed in figure 29 where diagnostic traits are labeled. See text and table 52.

O. laticeps). Presence of the modified cephalic arterial pattern and a different occlusal molar conformation (short paraflexus and two fossettes on second upper molar, short hypoflexid and fossettid on lower) isolate members of the *O. yunganus* group (*O. yunganus* and *O. tatei*). A complete carotid arterial pattern (sphenofrontal foramen and squamosoalisphenoid groove present) combined with the *megacephalus* molar occlusal configuration defines the trans-Andean species (*O. bolivaris* and *O. talamancae*). The primitive cephalic arterial circulation along with the molar occlusal pattern seen in *O. yunganus* (which may also be primitive) sets apart the *O. nitidus* group (*O. nitidus*, *O. macconnelli*, *O. emmonsae*, and *O. russatus*). Within each group, the species can be identified by either discrete traits, quantitative and proportional features, or a combination of both. *Oryzomys alfaroi*, the transforming player in Hershkovitz's evolutionary scenario, can also be objectively diagnosed as a real entity distinct from the other 10 species.

Integral to the insoluble nature of the former *Oryzomys* ''*capito*'' complex that prevailed among mammalogists before 1976 was the notion of a messy nomenclature. Some of the scientific names proposed in the 1800s seemed unidentifiable because the original descriptions are vague by current standards of description and did not appear to be based on existing types. Without name-bearing specimens at hand, the perceived nomenclatural problems were assumed to be unresolvable. This, too, we discovered, was a myth. Specimens upon which some of these older names are based still exist in collections of European museums, but were not identified specifically as types. We have been able to match original descriptions with series and designate lectotypes. Specimens apparently do not exist for only two taxa discussed in our report, and for these we designate neotypes.

Inferring phylogenetic relationships among the ten species defined here is beyond the scope of our report. However, while sorting specimens and analyzing data, we obtained strong impressions about possible relationships among the species based on overall morphological resemblances, observations that will eventually have to be tested. For example, members of the *Oryzomys megacephalus* and *O. yunganus* groups seem much alike compared with the other clusters. Were it not for the distinction between the two provided by molar occlusal patterns, we would confidently include *O. yunganus* and *O. tatei* along with *O. megacephalus* and *O. laticeps* in one group apart from the trans-Andean species, which seem to form a tight morphological cluster despite their striking external differences, and members of the *O. nitidus* group.

The diagnoses and distributions of particular species we present here acknowledge uncertainties regarding their actual morphological and geographic limits. Nevertheless, some biogeographic insights are beginning to emerge with systematic refinement of oryzomyine species and a fresh view of their distributions based on vouchered specimens. The Amazon Basin, with its vast reaches of verdant lowland rain forest, has apparently served as a cradle for the differentiation of some species of *Oryzomys* reviewed herein; the ranges of *O. macconnelli* and *O. yunganus* are essentially coterminous with Amazonia, and the geographic occurrences of others are restricted to areas within the Basin, whether toward its western (*O. nitidus* and *O. tatei*) or eastern (*O. emmonsae*) limits. Moreover, *O. megacephalus* is ubiquitous throughout Amazonia, although its populations also reach eastern Paraguay, and its probable closest relative, *O. laticeps*, occurs in Atlantic rain forest of southeastern Brazil. The morphologically similar *yunganus* and *megacephalus* groups are autochthonous to the Amazon Basin and Amazon Basin–Atlantic Forest, respectively. The mostly allopatric distributions of certain members of the *nitidus* group, namely *O. nitidus* and *O. russatus*, similarly span parts of these two South American realms and have the aspect of vicariant sister species. Corroboration of this hypothesis and determination of their cladistic relationship to the other Amazonian species, *O. emmonsae* and *O. macconnelli*, invite investigation with other kinds of data. However, the affinities of species that inhabit trans-Andean rainforest formations, stretching to the north and west of the Andean cordilleras, must be simultaneously considered in illuminating the phyletic diversification of the *nitidus* group (not only the species *O. bolivaris* and *O. talamancae* that we studied, but also Middle American forms such as *O. alfaroi*, *O. melanotis*, and *O. rostratus*).

To caution that the foregoing sketches of geographic pattern and phylogenetic origin require firmer empirical documentation of range and robust analyses of kinship is axiomatic. Attention is regularly drawn throughout our accounts to the huge swaths of lowland tropical forest devoid of any mammalian field inventory (see Voss and Emmons, 1996, for a rigorous overview of such inadequacies). To be sure, additional series from unsampled regions are needed to resolve the biological significance of the geographic patterns of morphological variation documented for *Oryzomys megacephalus*, *O. yunganus*, and *O. russatus*. Still, even so preliminary a view of oryzomyine systematics highlights the important originative role of the Amazon Basin and other lowland rainforest biomes. Admitting the obvious need for further revision of other species (*O. megacephalus*, *O. yunganus*, and *O. russatus*) and other genera (*Neacomys*, *Nectomys*, *Oecomys*, and *Oligoryzomys*), the number of rodent species known to be indigenous to Amazonia will surely increase. Such a picture of species richness and endemicity stands at odds with certain notions about Amazonian biodiversity (for example, Mares, 1992; but see Voss and Emmons, 1996, for a counterview).

We are impressed with how much still needs to be learned about Neotropical oryzomyines. Our report represents only a beginning, an understanding in the museum of the first lesson in the forest.

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APPENDIX A

Descriptive Statistics for Cranial and Dental Measurements (mm) of the *Oryzomys megacephalus* Complex

Below we list measurements of samples of *Oryzomys megacephalus* and *O. laticeps*, two remaining components of the former *O. "capito"* complex. Most of the geographic range of the complex is represented by samples consisting of specimens from one or more localities, which are identified in table 1. The holotype of *perenensis* is indicated by name in bold type. Specimens measured are listed in appendix B. Only adults (young to old) were used.

Sample	*N*	Mean ± SD	Observed range
Occipitonasal length			
FRENCH GUIANA	44	30.9 ± 0.93	29.3–32.5
SURINAM	7	30.6 ± 0.95	29.8–32.4
GUYANA: Barima-Waini	13	30.5 ± 1.10	28.3–32.2
GUYANA: Takutu-Essequibo	3	31.3 ± 0.92	30.3–32.1
VENEZUELA: Bolívar-1	32	31.1 ± 0.87	29.8–33.2
VENEZUELA: Bolívar-2	22	31.3 ± 0.89	30.2–33.3
VENEZUELA: Amazonas	9	32.2 ± 1.04	30.4–33.5
TRINIDAD	41	31.4 ± 1.01	29.2–33.7
COLOMBIA: Cundinamarca	23	33.1 ± 1.06	31.7–36.0
ECUADOR: Napo + Pastaza	32	33.9 ± 1.16	31.7–36.7
ECUADOR: Zamora-Chinchipe	2	32.6 ± 0.42	32.3–32.9
PERÚ: Loreto	2	33.4 ± 0.40	34.0–33.5
PERÚ: Pasco	21	35.0 ± 1.01	33.0–36.7
PERÚ: Junín (***perenensis***)	1	34.3	
PERÚ: Ucayali	22	32.9 ± 1.78	29.9–36.3
BOLIVIA: Pando-1	10	32.9 ± 0.63	31.8–33.8
BOLIVIA: Pando-2	1	34.2	
BOLIVIA: Beni	32	33.7 ± 1.15	31.7–36.5
BOLIVIA: Cochabamba	2	31.3 ± 0.64	30.8–31.7
BOLIVIA: Santa Cruz	10	32.5 ± 0.84	31.3–33.4
BRAZIL: Acre-1	5	33.5 ± 0.88	32.5–34.8
BRAZIL: Acre-2	20	33.7 ± 1.00	31.6–35.6
BRAZIL: Acre-3	21	32.9 ± 1.40	30.8–34.8
BRAZIL: Acre-4	5	33.3 ± 0.79	32.1–34.0
BRAZIL: Acre-5	7	34.5 ± 0.71	33.5–35.7
BRAZIL: Amazonas-1	15	34.3 ± 1.36	31.6–36.9
BRAZIL: Amazonas-2	17	33.3 ± 1.15	31.4–35.7
BRAZIL: Amazonas-3	29	33.7 ± 1.14	31.2–35.5
BRAZIL: Amazonas-4	18	33.4 ± 1.62	31.2–37.9
BRAZIL: Amazonas-5	35	33.1 ± 1.26	31.1–36.3
BRAZIL: Amazonas-6	26	33.6 ± 1.21	31.4–36.5
BRAZIL: Amazonas-7	24	34.0 ± 1.42	31.7–36.8
BRAZIL: Amazonas-8	13	33.8 ± 1.21	32.0–36.3
BRAZIL: Amazonas-9	2	32.3 ± 0.42	32.0–32.6
BRAZIL: Mato Grosso-2	26	29.8 ± 0.92	28.5–32.3
BRAZIL: Goiás	11	31.5 ± 0.51	30.6–32.3
BRAZIL: Federal District	10	32.6 ± 0.65	31.6–33.8
BRAZIL: Pará-1	29	32.3 ± 1.44	30.1–34.2
BRAZIL: Pará-2	16	31.4 ± 1.31	29.3–33.5
BRAZIL: Pará-3	9	31.3 ± 0.72	30.4–32.5
BRAZIL: Pará-4	36	29.7 ± 0.78	27.2–31.5
BRAZIL: Amapá	44	31.2 ± 1.01	29.4–33.9
PARAGUAY	13	32.5 ± 1.42	30.5–34.9
BRAZIL: Pernambuco	4	35.4 ± 1.02	33.9–36.1
BRAZIL: Bahia	3	34.3 ± 0.25	34.1–34.4
BRAZIL: Espírito Santo	3	33.8 ± 0.55	33.4–34.4
Zygomatic breadth			
FRENCH GUIANA	44	15.2 ± 0.21	14.2–16.4
SURINAM	7	15.1 ± 0.55	14.3–15.8
GUYANA: Barima-Waini	13	15.4 ± 0.38	14.8–16.1
GUYANA: Takutu-Essequibo	3	15.6 ± 0.51	15.2–16.2
VENEZUELA: Bolívar-1	32	15.6 ± 0.59	14.4–16.8
VENEZUELA: Bolívar-2	22	15.8 ± 0.55	14.8–17.1
VENEZUELA: Amazonas	9	16.2 ± 0.42	15.3–16.7
TRINIDAD	41	15.6 ± 0.59	13.8–16.7
COLOMBIA: Cundinamarca	23	16.0 ± 0.54	15.1–17.5
ECUADOR: Napo + Pastaza	32	16.9 ± 0.82	15.1–18.5
ECUADOR: Zamora-Chinchipe	2	16.4 ± 0.71	15.9–16.9
PERÚ: Loreto	2	17.0 ± 0.64	16.5–17.4
PERÚ: Pasco	21	17.1 ± 0.63	16.2–18.3
PERÚ: Junín (***perenensis***)	1	17.5	
PERÚ: Ucayali	22	16.6 ± 0.86	15.2–18.2
BOLIVIA: Pando-1	10	16.7 ± 0.56	15.6–17.2
BOLIVIA: Pando-2	1	17.4	
BOLIVIA: Beni	32	17.4 ± 0.70	16.2–18.9
BOLIVIA: Cochabamba	2	16.1 ± 0.35	15.8–16.3
BOLIVIA: Santa Cruz	10	16.5 ± 0.64	15.3–17.7
BRAZIL: Acre-1	5	17.1 ± 0.48	16.4–17.6
BRAZIL: Acre-2	20	17.0 ± 0.71	15.7–18.5
BRAZIL: Acre-3	21	16.5 ± 0.74	15.1–18.5
BRAZIL: Acre-4	5	16.9 ± 0.51	16.2–17.4
BRAZIL: Acre-5	7	17.2 ± 0.49	16.6–17.9
BRAZIL: Amazonas-1	15	17.3 ± 0.72	16.2–18.7
BRAZIL: Amazonas-2	17	16.9 ± 0.65	16.0–18.3
BRAZIL: Amazonas-3	29	17.1 ± 0.62	16.0–18.2
BRAZIL: Amazonas-4	18	16.8 ± 0.83	16.0–19.0
BRAZIL: Amazonas-5	35	16.4 ± 0.84	14.5–17.9
BRAZIL: Amazonas-6	26	17.0 ± 0.77	15.5–18.8

Sample	*N*	Mean ± SD	Observed range
BRAZIL: Amazonas-7	24	17.0 ± 0.72	15.8–18.5
BRAZIL: Amazonas-8	13	16.9 ± 0.59	16.2–18.3
BRAZIL: Amazonas-9	2	15.7 ± 0.00	—
BRAZIL: Mato Grosso-2	26	15.1 ± 0.62	14.0–16.5
BRAZIL: Goiás	11	16.1 ± 0.47	15.2–16.6
BRAZIL: Federal District	10	16.7 ± 0.59	16.0–17.9
BRAZIL: Pará-1	29	16.4 ± 0.76	15.0–18.1
BRAZIL: Pará-2	16	15.6 ± 0.22	14.4–16.7
BRAZIL: Pará-3	9	15.8 ± 0.68	14.8–17.0
BRAZIL: Pará-4	36	15.0 ± 0.49	13.9–15.9
BRAZIL: Amapá	44	15.3 ± 0.54	14.5–16.5
PARAGUAY	13	16.6 ± 0.85	15.1–17.7
BRAZIL: Pernambuco	4	17.5 ± 0.77	16.7–18.4
BRAZIL: Bahia	3	17.1 ± 0.31	16.8–17.4
BRAZIL: Espírito Santo	3	17.1 ± 0.59	16.4–17.5

Interorbital breadth

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	5.1 ± 0.21	4.7–5.6
SURINAM	7	4.8 ± 0.14	4.6–5.0
GUYANA: Barima-Waini	13	5.0 ± 0.25	4.5–5.3
GUYANA: Takutu-Essequibo	3	5.2 ± 0.25	5.0–5.5
VENEZUELA: Bolívar-1	32	5.1 ± 0.17	4.9–5.5
VENEZUELA: Bolívar-2	22	5.3 ± 0.13	5.0–5.5
VENEZUELA: Amazonas	9	4.9 ± 0.22	4.5–5.2
TRINIDAD	41	5.1 ± 0.18	4.8–5.5
COLOMBIA: Cundinamarca	23	5.1 ± 0.23	4.7–5.7
ECUADOR: Napo + Pastaza	34	5.3 ± 0.26	4.9–6.1
ECUADOR: Zamora-Chinchipe	2	5.2 ± 0.21	5.0–5.3
PERÚ: Loreto	2	5.1 ± 0.14	5.0–5.2
PERÚ: Pasco	21	5.5 ± 0.20	5.2–6.0
PERÚ: Junín (***perenensis***)	1	5.2	
PERÚ: Ucayali	22	5.1 ± 0.26	4.4–5.8
BOLIVIA: Pando-1	10	5.1 ± 0.16	4.8–5.4
BOLIVIA: Pando-2	1	5.0	
BOLIVIA: Beni	32	5.0 ± 0.20	4.7–5.5
BOLIVIA: Cochabamba	2	5.3 ± 0.21	5.1–5.4
BOLIVIA: Santa Cruz	10	5.2 ± 0.13	5.0–5.4
BRAZIL: Acre-1	5	5.1 ± 0.20	4.9–5.0
BRAZIL: Acre-2	20	5.3 ± 0.15	4.9–5.5
BRAZIL: Acre-3	21	5.2 ± 0.27	4.6–5.7
BRAZIL: Acre-4	5	5.1 ± 0.17	5.0–5.4
BRAZIL: Acre-5	7	5.3 ± 0.15	5.1–5.4
BRAZIL: Amazonas-1	15	5.3 ± 0.19	4.9–5.7
BRAZIL: Amazonas-2	17	5.3 ± 0.25	5.0–5.7
BRAZIL: Amazonas-3	29	5.3 ± 0.29	4.5–5.8
BRAZIL: Amazonas-4	18	5.2 ± 0.29	4.4–5.5
BRAZIL: Amazonas-5	35	5.3 ± 0.29	4.9–6.2
BRAZIL: Amazonas-6	26	5.3 ± 0.23	4.9–5.9
BRAZIL: Amazonas-7	24	5.4 ± 0.24	4.9–5.8
BRAZIL: Amazonas-8	13	5.4 ± 0.15	5.1–5.5
BRAZIL: Amazonas-9	2	5.0 ± 0.42	4.7–5.3
BRAZIL: Mato Grosso-2	26	4.8 ± 0.21	4.4–5.2
BRAZIL: Goiás	11	5.2 ± 0.14	5.0–5.4
BRAZIL: Federal District	10	5.3 ± 0.18	5.1–5.6
BRAZIL: Pará-1	29	5.1 ± 0.23	4.6–5.6
BRAZIL: Pará-2	16	5.0 ± 0.22	4.7–5.4
BRAZIL: Pará-3	9	4.8 ± 0.22	4.6–5.1
BRAZIL: Pará-4	36	4.8 ± 0.14	4.4–5.0
BRAZIL: Amapá	44	5.1 ± 0.19	4.8–5.7
PARAGUAY	13	5.1 ± 0.17	4.7–5.3
BRAZIL: Pernambuco	4	5.4 ± 0.25	5.1–5.7
BRAZIL: Bahia	3	5.3 ± 0.17	5.1–5.4
BRAZIL: Espírito Santo	3	5.2 ± 0.15	5.0–5.3

Length of rostrum

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	9.8 ± 0.45	9.0–10.6
SURINAM	7	9.8 ± 0.42	9.4–10.5
GUYANA: Barima-Waini	13	9.6 ± 0.46	8.6–10.1
GUYANA: Takutu-Essequibo	3	9.8 ± 0.25	9.6–10.1
VENEZUELA: Bolívar-1	32	9.8 ± 0.46	8.9–10.8
VENEZUELA: Bolívar-2	22	10.0 ± 0.51	9.2–10.9
VENEZUELA: Amazonas	9	10.1 ± 0.49	9.1–10.6
TRINIDAD	41	9.9 ± 0.43	9.0–11.0
COLOMBIA: Cundinamarca	23	10.6 ± 0.46	9.8–11.7
ECUADOR: Napo + Pastaza	34	10.6 ± 0.49	9.8–11.8
ECUADOR: Zamora-Chinchipe	2	10.1 ± 0.14	10.0–10.2
PERÚ: Loreto	2	10.6 ± 0.50	10.4–11.1
PERÚ: Pasco	21	11.0 ± 0.43	10.1–11.6
PERÚ: Junín (***perenensis***)	1	10.8	
PERÚ: Ucayali	22	10.4 ± 0.83	9.2–11.9
BOLIVIA: Pando-1	10	10.3 ± 0.29	9.8–10.7
BOLIVIA: Pando-2	1	10.5	
BOLIVIA: Beni	32	10.4 ± 0.50	9.6–11.9
BOLIVIA: Cochabamba	2	9.9 ± 0.71	9.4–10.4
BOLIVIA: Santa Cruz	10	10.1 ± 0.38	9.6–10.6
BRAZIL: Acre-1	5	10.5 ± 0.61	9.7–11.3
BRAZIL: Acre-2	20	10.5 ± 0.49	9.7–11.9
BRAZIL: Acre-3	21	10.3 ± 0.59	9.3–11.5
BRAZIL: Acre-4	5	10.3 ± 0.27	10.0–10.7
BRAZIL: Acre-5	7	10.7 ± 0.24	10.3–11.0
BRAZIL: Amazonas-1	15	10.7 ± 0.73	9.2–12.2
BRAZIL: Amazonas-2	17	10.2 ± 0.55	8.9–11.2
BRAZIL: Amazonas-3	29	10.3 ± 0.59	9.0–11.5
BRAZIL: Amazonas-4	18	10.4 ± 0.66	9.3–12.2
BRAZIL: Amazonas-5	35	10.4 ± 0.54	9.3–11.4
BRAZIL: Amazonas-6	26	10.3 ± 0.48	9.2–11.1
BRAZIL: Amazonas-7	24	10.6 ± 0.66	9.7–12.0
BRAZIL: Amazonas-8	13	10.5 ± 0.74	9.3–11.5
BRAZIL: Amazonas-9	2	10.4 ± 0.07	10.3–10.4
BRAZIL: Mato Grosso-2	26	9.1 ± 0.47	8.4–10.0
BRAZIL: Goiás	11	10.0 ± 0.25	9.6–10.4
BRAZIL: Federal District	10	10.3 ± 0.29	9.7–10.7

Sample	*N*	Mean ± SD	Observed range
BRAZIL: Pará-1	29	10.2 ± 0.50	9.4–11.2
BRAZIL; Pará-2	16	9.9 ± 0.50	9.1–10.6
BRAZIL: Pará-3	9	9.8 ± 0.42	9.3–10.6
BRAZIL: Pará-4	36	9.1 ± 0.41	8.3–9.9
BRAZIL: Amapá	44	10.1 ± 0.52	9.1–11.1
PARAGUAY	13	10.3 ± 0.61	9.4–11.1
BRAZIL: Pernambuco	4	11.5 ± 0.74	10.4–12.1
BRAZIL: Bahia	3	10.9 ± 0.31	10.6–11.2
BRAZIL: Espírito Santo	3	10.2 ± 0.75	9.5–11.0

Breadth of rostrum

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	6.2 ± 0.31	5.6–6.9
SURINAM	7	6.0 ± 0.44	5.5–6.6
GUYANA: Barima-Waini	13	5.9 ± 0.36	5.4–6.4
GUYANA: Takutu-Essequibo	3	6.2 ± 0.30	5.9–6.5
VENEZUELA: Bolívar-1	32	6.1 ± 0.32	5.6–7.0
VENEZUELA: Bolívar-2	22	6.0 ± 0.35	5.4–6.9
VENEZUELA: Amazonas	9	6.4 ± 0.16	6.1–6.6
TRINIDAD	41	5.8 ± 0.33	5.3–6.8
COLOMBIA: Cundinamarca	23	6.2 ± 0.38	5.5–7.4
ECUADOR: Napo + Pastaza	33	6.3 ± 0.42	5.7–7.4
ECUADOR: Zamora-Chinchipe	2	6.3 ± 0.14	6.2–6.4
PERÚ: Loreto	2	6.5 ± 0.10	6.4–6.5
PERÚ: Pasco	21	7.0 ± 0.35	6.3–7.5
PERÚ: Junín (***perenensis***)	1	6.7	
PERÚ: Ucayali	22	6.3 ± 0.44	5.6–6.9
BOLIVIA: Pando-1	10	6.4 ± 0.40	5.8–7.0
BOLIVIA: Pando-2	1	6.6	
BOLIVIA: Beni	32	6.6 ± 0.41	5.7–7.5
BOLIVIA: Cochabamba	2	6.0 ± 0.00	—
BOLIVIA: Santa Cruz	10	6.2 ± 0.31	5.7–6.7
BRAZIL: Acre-1	5	6.2 ± 0.20	5.9–6.3
BRAZIL: Acre-2	20	6.5 ± 0.49	5.6–7.5
BRAZIL: Acre-3	21	6.3 ± 0.46	5.3–7.5
BRAZIL: Acre-4	5	6.2 ± 0.25	6.0–6.6
BRAZIL: Acre-5	7	6.7 ± 0.37	5.9–7.0
BRAZIL: Amazonas-1	15	6.6 ± 0.38	6.0–7.2
BRAZIL: Amazonas-2	17	6.4 ± 0.41	5.8–7.4
BRAZIL: Amazonas-3	29	6.4 ± 0.30	5.6–7.0
BRAZIL: Amazonas-4	18	6.4 ± 0.63	5.5–7.6
BRAZIL: Amazonas-5	35	6.4 ± 0.55	5.5–8.4
BRAZIL: Amazonas-6	26	6.3 ± 0.47	5.8–7.6
BRAZIL: Amazonas-7	24	6.4 ± 0.44	5.8–7.6
BRAZIL: Amazonas-8	13	6.6 ± 0.33	5.9–7.0
BRAZIL: Amazonas-9	2	6.2 ± 0.14	6.1–6.3
BRAZIL: Mato Grosso-2	26	5.6 ± 0.34	5.1–6.4
BRAZIL: Goiás	11	6.2 ± 0.28	5.7–6.8
BRAZIL: Federal District	10	6.3 ± 0.29	5.9–6.7
BRAZIL: Pará-1	29	6.4 ± 0.50	5.4–7.3
BRAZIL: Pará-2	16	6.2 ± 0.43	5.7–6.8
BRAZIL: Pará-4	36	5.8 ± 0.32	5.1–6.5
BRAZIL: Pará-7	13	6.0 ± 0.33	5.2–6.5
BRAZIL: Amapá	44	5.9 ± 0.37	5.1–6.7
PARAGUAY	13	6.3 ± 0.44	5.5–6.9
BRAZIL: Pernambuco	4	6.7 ± 0.45	6.0–6.9
BRAZIL: Bahia	3	6.8 ± 0.17	6.7–7.0
BRAZIL: Espírito Santo	3	6.7 ± 0.20	6.5–6.9

Lambdoidal breadth

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	11.6 ± 0.34	10.6–12.3
SURINAM	7	11.3 ± 0.35	11.0–11.9
GUYANA: Barima-Waini	13	11.5 ± 0.42	10.9–12.1
GUYANA: Takutu-Essequibo	3	11.9 ± 0.31	11.6–12.2
VENEZUELA: Bolívar-1	32	11.6 ± 0.37	10.5–12.4
VENEZUELA: Bolívar-2	22	11.8 ± 0.35	11.2–12.6
VENEZUELA: Amazonas	9	12.1 ± 0.43	11.7–13.0
TRINIDAD	41	11.8 ± 0.38	10.9–12.7
COLOMBIA: Cundinamarca	23	12.2 ± 0.32	11.5–13.1
ECUADOR: Napo + Pastaza	30	12.4 ± 0.58	11.5–13.8
ECUADOR: Zamora-Chinchipe	2	12.4 ± 0.07	12.3–12.4
PERÚ: Loreto	2	12.1 ± 0.10	12.1–12.2
PERÚ: Pasco	21	12.7 ± 0.33	11.9–13.3
PERÚ: Junín (***perenensis***)	1	12.8	
PERÚ: Ucayali	22	12.1 ± 0.55	11.3–13.1
BOLIVIA: Pando-1	10	12.1 ± 0.28	11.8–12.7
BOLIVIA: Pando-2	1	12.5	
BOLIVIA: Beni	32	12.7 ± 0.56	11.8–13.8
BOLIVIA: Cochabamba	2	11.7 ± 0.00	—
BOLIVIA: Santa Cruz	10	12.2 ± 0.23	11.9–12.6
BRAZIL: Acre-1	5	12.3 ± 0.17	12.0–12.4
BRAZIL: Acre-2	20	12.4 ± 0.50	11.6–13.6
BRAZIL: Acre-3	21	12.1 ± 0.44	11.5–13.1
BRAZIL: Acre-4	5	12.3 ± 0.16	12.1–12.5
BRAZIL: Acre-5	7	12.6 ± 0.44	12.1–13.3
BRAZIL: Amazonas-1	15	12.4 ± 0.45	11.8–13.2
BRAZIL: Amazonas-2	17	12.3 ± 0.45	11.6–13.2
BRAZIL: Amazonas-3	29	12.6 ± 0.42	11.8–13.3
BRAZIL: Amazonas-4	18	12.3 ± 0.31	11.8–13.0
BRAZIL: Amazonas-5	35	12.3 ± 0.46	11.0–13.2
BRAZIL: Amazonas-6	26	12.3 ± 0.43	11.5–12.9
BRAZIL: Amazonas-7	24	12.4 ± 0.45	11.6–13.4
BRAZIL: Amazonas-8	13	12.3 ± 0.48	11.3–13.1
BRAZIL: Amazonas-9	2	10.9 ± 0.85	10.3–11.5
BRAZIL: Mato Grosso-2	26	11.3 ± 0.40	10.6–12.0
BRAZIL: Goiás	11	11.6 ± 0.37	11.2–12.2
BRAZIL: Federal District	10	12.3 ± 0.35	11.6–12.8
BRAZIL: Pará-1	29	11.8 ± 0.59	10.7–13.0
BRAZIL: Pará-2	16	11.3 ± 0.45	10.5–12.0
BRAZIL: Pará-3	9	11.5 ± 0.37	10.9–12.0
BRAZIL: Pará-4	36	11.2 ± 0.48	10.4–12.0
BRAZIL: Amapá	44	11.5 ± 0.33	10.9–12.2
PARAGUAY	13	11.9 ± 0.39	11.3–12.5

Sample	*N*	Mean ± SD	Observed range
BRAZIL: Pernambuco	4	12.8 ± 0.28	12.6–13.2
BRAZIL: Bahia	3	12.4 ± 0.31	12.1–12.7
BRAZIL: Espírito Santo	3	12.4 ± 0.23	12.1–12.5
Height of braincase			
FRENCH GUIANA	44	8.5 ± 0.31	7.9–9.1
SURINAM	7	8.2 ± 0.29	7.9–8.6
GUYANA: Barima-Waini	13	8.3 ± 0.33	7.7–9.1
GUYANA: Takutu-Essequibo	3	8.3 ± 0.31	8.0–8.6
VENEZUELA: Bolívar-1	32	8.6 ± 0.37	8.0–9.5
VENEZUELA: Bolívar-1	22	8.6 ± 0.39	7.8–9.5
VENEZUELA: Amazonas	9	8.6 ± 0.23	8.2–9.0
TRINIDAD	41	8.5 ± 0.32	7.8–9.4
COLOMBIA: Cundinamarca	23	8.7 ± 0.33	8.1–9.6
ECUADOR: Napo + Pastaza	29	9.1 ± 0.49	8.0–10.2
ECUADOR: Zamora-Chinchipe	2	8.8 ± 0.42	8.5–9.1
PERÚ: Loreto	2	9.3 ± 0.20	9.1–9.4
PERÚ: Pasco	21	9.3 ± 0.38	8.6–9.9
PERÚ: Junín (***perenensis***)	1	9.2	
PERÚ: Ucayali	22	8.9 ± 0.41	8.3–9.9
BOLIVIA: Pando-1	10	9.0 ± 0.42	8.5–9.8
BOLIVIA: Pando-2	1	9.1	
BOLIVIA: Beni	32	9.2 ± 0.35	8.6–9.9
BOLIVIA: Cochabamba	2	9.5 ± 0.71	8.0–9.0
BOLIVIA: Santa Cruz	10	9.0 ± 0.32	8.9–9.5
BRAZIL: Acre-1	5	9.1 ± 0.16	8.9–9.3
BRAZIL: Acre-2	20	9.4 ± 0.50	8.2–10.4
BRAZIL: Acre-3	21	8.9 ± 0.43	8.3–9.9
BRAZIL: Acre-4	5	9.0 ± 0.24	8.7–9.3
BRAZIL: Acre-5	7	9.1 ± 0.28	8.8–9.5
BRAZIL: Amazonas-1	15	9.1 ± 0.39	8.3–9.7
BRAZIL: Amazonas-2	17	9.2 ± 0.47	8.4–9.5
BRAZIL: Amazonas-3	29	9.1 ± 0.27	8.6–9.7
BRAZIL: Amazonas-4	18	8.9 ± 0.37	8.3–9.6
BRAZIL: Amazonas-5	35	9.0 ± 0.41	8.1–9.7
BRAZIL: Amazonas-6	26	9.0 ± 0.35	8.4–9.7
BRAZIL: Amazonas-7	24	9.0 ± 0.41	8.0–9.8
BRAZIL: Amazonas-8	13	9.0 ± 0.35	8.3–9.5
BRAZIL: Amazonas-9	2	8.3 ± 0.28	8.1–8.5
BRAZIL: Mato Grosso-2	26	8.2 ± 0.36	7.6–9.0
BRAZIL: Goiás	11	8.5 ± 0.22	8.2–9.0
BRAZIL: Federal District	10	8.9 ± 0.34	8.2–9.2
BRAZIL: Pará-1	29	8.6 ± 0.48	7.8–10.0
BRAZIL: Pará-2	16	8.4 ± 0.26	8.0–8.9
BRAZIL: Pará-3	9	8.4 ± 0.38	7.8–8.8
BRAZIL: Pará-4	36	8.0 ± 0.27	7.4–8.7
BRAZIL: Amapá	44	8.4 ± 0.33	7.9–9.5
PARAGUAY	13	8.7 ± 0.34	8.1–9.3
BRAZIL: Pernambuco	4	9.3 ± 0.30	8.8–9.5
BRAZIL: Bahia	3	8.9 ± 0.23	8.8–9.2
BRAZIL: Espírito Santo	3	8.9 ± 0.10	8.8–9.0
Breadth of zygomatic plate			
FRENCH GUIANA	44	3.1 ± 0.27	2.5–3.7
SURINAM	7	3.1 ± 0.20	2.8–3.4
GUYANA: Barima-Waini	13	3.2 ± 0.26	2.7–3.5
GUYANA: Takutu-Essequibo	3	3.5 ± 0.21	3.3–3.7
VENEZUELA: Bolívar-1	32	3.3 ± 0.29	2.8–4.0
VENEZUELA: Bolívar-2	22	3.2 ± 0.22	2.8–3.6
VENEZUELA: Amazonas	9	3.4 ± 0.14	3.2–3.6
TRINIDAD	41	3.2 ± 0.23	2.8–3.6
COLOMBIA: Cundinamarca	23	3.5 ± 0.23	3.0–4.0
ECUADOR: Napo + Pastaza	34	3.8 ± 0.26	3.3–4.3
ECUADOR: Zamora-Chinchipe	2	3.7 ± 0.28	3.5–3.9
PERÚ: Loreto	2	4.0 ± 0.50	3.6–4.3
PERÚ: Pasco	21	3.9 ± 0.25	3.5–4.4
PERÚ: Junín (***perenensis***)	1	3.7	
PERÚ: Ucayali	22	3.6 ± 0.44	2.8–4.4
BOLIVIA: Pando-1	10	3.6 ± 0.21	3.4–4.0
BOLIVIA: Pando-2	1	4.0	
BOLIVIA: Beni	32	4.0 ± 0.22	3.6–4.3
BOLIVIA: Cochabamba	2	3.4 ± 0.21	3.2–3.5
BOLIVIA: Santa Cruz	10	3.6 ± 0.23	3.4–4.1
BRAZIL: Acre-1	5	3.7 ± 0.16	3.5–3.9
BRAZIL: Acre-2	20	3.7 ± 0.23	3.3–4.1
BRAZIL: Acre-3	21	3.5 ± 0.27	3.0–4.0
BRAZIL: Acre-4	5	3.4 ± 0.08	3.3–3.5
BRAZIL: Acre-5	7	3.8 ± 0.14	3.6–3.9
BRAZIL: Amazonas-1	15	3.9 ± 0.32	3.2–4.3
BRAZIL: Amazonas-2	17	3.6 ± 0.25	3.1–4.2
BRAZIL: Amazonas-3	29	3.7 ± 0.18	3.3–4.0
BRAZIL: Amazonas-4	18	3.6 ± 0.27	3.1–4.2
BRAZIL: Amazonas-5	35	3.5 ± 0.25	3.0–4.1
BRAZIL: Amazonas-6	26	3.6 ± 0.22	3.2–4.1
BRAZIL: Amazonas-7	24	3.7 ± 0.26	3.0–4.1
BRAZIL: Amazonas-8	13	3.7 ± 0.17	3.4–3.9
BRAZIL: Amazonas-9	2	3.7 ± 0.21	3.5–3.8
BRAZIL: Mato Grosso-2	26	3.1 ± 0.25	2.7–3.7
BRAZIL: Goiás	11	3.3 ± 0.14	3.0–3.5
BRAZIL: Federal District	10	3.6 ± 0.30	3.1–4.0
BRAZIL: Pará-1	29	3.6 ± 0.27	2.9–4.1
BRAZIL: Pará-2	16	3.3 ± 0.26	2.8–3.8
BRAZIL: Pará-3	9	3.2 ± 0.27	3.0–3.8
BRAZIL: Pará-4	36	3.2 ± 0.21	2.7–3.6
BRAZIL: Amapá	44	3.3 ± 0.17	2.9–3.6
PARAGUAY	13	3.3 ± 0.29	3.0–3.8
BRAZIL: Pernambuco	4	3.7 ± 0.25	3.4–4.0
BRAZIL: Bahia	3	3.8 ± 0.06	3.8–3.9
BRAZIL: Espírito Santo	3	3.9 ± 0.12	3.8–4.0
Length of diastema			
FRENCH GUIANA	44	7.8 ± 0.38	6.9–8.5
SURINAM	7	7.8 ± 0.51	7.4–8.6

Sample	*N*	Mean ± SD	Observed range
TRINIDAD	41	10.6 ± 0.53	9.5–12.0
COLOMBIA: Cundinamarca	23	11.1 ± 0.44	10.2–12.2
ECUADOR: Napo + Pastaza	29	11.6 ± 0.52	11.0–13.1
ECUADOR: Zamora-Chinchipe	2	11.2 ± 0.35	10.9–11.4
PERÚ: Loreto	2	11.7 ± 0.10	11.6–11.8
PERÚ: Pasco	21	11.7 ± 0.50	10.9–12.6
PERÚ: Junín (***perenensis***)	1	11.2	
PERÚ: Ucayali	22	10.9 ± 0.70	9.8–12.6
BOLIVIA: Pando-1	10	11.0 ± 0.40	10.3–11.6
BOLIVIA: Pando-2	1	11.9	
BOLIVIA: Beni	32	11.4 ± 0.55	10.2–12.5
BOLIVIA: Cochabamba	2	10.2 ± 0.14	10.1–10.3
BOLIVIA: Santa Cruz	10	11.0 ± 0.42	11.0–11.4
BRAZIL: Acre-1	5	11.3 ± 0.41	10.6–11.6
BRAZIL: Acre-2	20	11.4 ± 0.65	10.0–12.5
BRAZIL: Acre-3	21	10.8 ± 0.65	9.7–12.0
BRAZIL: Acre-4	5	11.3 ± 0.49	10.8–11.9
BRAZIL: Acre-5	7	11.7 ± 0.32	11.2–12.1
BRAZIL: Amazonas-1	15	11.6 ± 0.66	10.3–12.5
BRAZIL: Amazonas-2	17	11.2 ± 0.49	10.5–12.2
BRAZIL: Amazonas-3	29	11.4 ± 0.48	10.5–12.4
BRAZIL: Amazonas-4	18	11.2 ± 0.71	10.5–13.2
BRAZIL: Amazonas-5	35	11.0 ± 0.59	9.9–12.1
BRAZIL: Amazonas-6	26	11.2 ± 0.66	10.1–12.6
BRAZIL: Amazonas-7	24	11.4 ± 0.54	10.4–12.3
BRAZIL: Amazonas-8	13	11.3 ± 0.53	10.6–12.4
BRAZIL: Amazonas-9	2	11.4 ± 0.35	11.1–11.6
BRAZIL: Mato Grosso-2	26	10.2 ± 0.41	9.5–11.0
BRAZIL: Goiás	11	10.9 ± 0.45	10.3–11.5
BRAZIL: Federal District	10	11.5 ± 0.54	10.8–12.4
BRAZIL: Pará-1	29	11.2 ± 0.72	9.7–12.5
BRAZIL: Pará-2	16	10.8 ± 0.71	9.5–11.8
BRAZIL: Pará-3	9	10.9 ± 9.42	10.4–11.5
BRAZIL: Pará-4	36	10.2 ± 0.35	9.4–11.1
BRAZIL: Amapá	44	10.5 ± 0.49	9.3–12.0
PARAGUAY	13	11.3 ± 0.68	10.1–12.4
BRAZIL: Pernambuco	4	12.0 ± 0.15	11.9–12.2
BRAZIL: Bahia	3	12.1 ± 0.32	11.9–12.5
BRAZIL: Espírito Santo	3	12.0 ± 0.29	11.8–12.3

Length of incisive foramina

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	4.4 ± 0.29	3.9–5.1
SURINAM	7	4.4 ± 0.14	4.2–4.6
GUYANA: Barima-Waini	13	4.6 ± 0.31	4.2–5.1
GUYANA: Takutu-Essequibo	3	4.6 ± 0.12	4.5–4.7
VENEZUELA: Bolívar-1	32	4.5 ± 0.25	3.9–4.8
VENEZUELA: Bolívar-2	22	4.3 ± 0.29	3.9–4.7
VENEZUELA: Amazonas	9	4.7 ± 0.35	4.1–5.2
TRINIDAD	41	4.6 ± 0.27	4.0–5.1
COLOMBIA: Cundinamarca	23	4.8 ± 0.23	4.2–5.5
ECUADOR: Napo + Pastaza	34	4.5 ± 0.31	4.0–5.3
ECUADOR: Zamora-Chinchipe	2	4.7 ± 0.64	4.2–5.1
PERÚ: Loreto	2	4.6 ± 0.40	4.3–4.8
PERÚ: Pasco	21	4.8 ± 0.30	4.1–5.4
PERÚ: Junín (***perenensis***)	1	4.8	
PERÚ: Ucayali	22	4.5 ± 0.31	4.0–5.2
BOLIVIA: Pando-1	10	4.5 ± 0.38	3.9–5.0
BOLIVIA: Pando-2	1	4.6	
BOLIVIA: Beni	32	4.6 ± 0.24	4.2–5.2
BOLIVIA: Cochabamba	2	4.4 ± 0.28	4.2–4.6
BOLIVIA: Santa Cruz	10	4.5 ± 0.16	4.2–4.8
BRAZIL: Acre-1	5	4.5 ± 0.28	4.2–4.9
BRAZIL: Acre-2	20	4.6 ± 0.25	4.1–5.1
BRAZIL: Acre-3	21	4.5 ± 0.30	3.8–4.9
BRAZIL: Acre-4	5	4.5 ± 0.39	4.0–5.0
BRAZIL: Acre-5	7	4.8 ± 0.39	4.2–5.2
BRAZIL: Amazonas-1	15	4.7 ± 0.21	4.3–5.0
BRAZIL: Amazonas-2	17	4.6 ± 0.37	4.0–5.2
BRAZIL: Amazonas-3	29	4.6 ± 0.34	4.0–5.3
BRAZIL: Amazonas-4	18	4.7 ± 0.38	4.2–5.2
BRAZIL: Amazonas-5	35	4.6 ± 0.30	3.8–5.2
BRAZIL: Amazonas-6	26	4.6 ± 0.32	4.0–5.4
BRAZIL: Amazonas-7	24	4.8 ± 0.32	4.1–5.4
BRAZIL: Amazonas-8	13	4.8 ± 0.37	3.9–5.3
BRAZIL: Amazonas-9	2	4.5 ± 0.07	4.4–4.5
BRAZIL: Mato Grosso-2	26	4.2 ± 0.33	3.4–4.7
BRAZIL: Goiás	11	4.4 ± 0.25	4.0–4.7
BRAZIL: Federal District	10	4.4 ± 0.39	3.9–5.2
BRAZIL: Pará-1	29	4.5 ± 0.31	3.9–5.4
BRAZIL: Pará-2	16	4.6 ± 0.32	4.0–5.2
BRAZIL: Pará-3	9	4.4 ± 0.28	4.1–4.8
BRAZIL: Pará-4	36	4.2 ± 0.23	3.5–4.6
BRAZIL: Amapá	44	4.4 ± 0.22	3.9–5.0
PARAGUAY	13	4.3 ± 0.30	3.8–4.9
BRAZIL: Pernambuco	4	5.0 ± 0.22	4.8–5.3
BRAZIL: Bahia	3	4.8 ± 0.21	4.6–5.0
BRAZIL: Espírito Santo	3	4.9 ± 0.25	4.6–5.1

Breadth of incisive foramina

Sample	*N*	Mean ± SD	Observed range
FRENCH GUIANA	44	2.3 ± 0.12	2.0–2.6
SURINAM	7	2.4 ± 0.19	2.2–2.7
GUYANA: Barima-Waini	13	2.2 ± 0.25	1.8–2.6
GUYANA: Takutu-Essequibo	3	2.4 ± 0.20	2.2–2.6
VENEZUELA: Bolívar-1	32	2.4 ± 0.15	2.0–2.7
VENEZUELA: Bolívar-2	22	2.3 ± 0.17	2.0–2.5
VENEZUELA: Amazonas	9	2.4 ± 0.17	2.3–2.8
TRINIDAD	41	2.3 ± 0.14	2.0–2.6
COLOMBIA: Cundinamarca	23	2.4 ± 0.16	2.1–2.7
ECUADOR: Napo + Pastaza	33	2.3 ± 0.18	2.0–2.7

Sample	*N*	Mean ± SD	Observed range
ECUADOR: Zamora-Chinchipe	2	2.2 ± 0.35	1.9–2.4
PERÚ: Loreto	2	2.5 ± 0.20	2.3–2.6
PERÚ: Pasco	21	2.3 ± 0.18	2.0–2.7
PERÚ: Junín (*perenensis*)	1	2.4	
PERÚ: Ucayali	22	2.4 ± 0.14	2.2–2.7
BOLIVIA: Pando-1	10	2.2 ± 0.21	1.9–2.6
BOLIVIA: Pando-2	1	2.3	
BOLIVIA: Beni	32	2.4 ± 0.14	2.1–2.6
BOLIVIA: Cochabamba	2	2.5 ± 0.07	2.4–2.5
BOLIVIA: Santa Cruz	10	2.4 ± 0.18	2.1–2.6
BRAZIL: Acre-1	5	2.2 ± 0.11	2.0–2.3
BRAZIL: Acre-2	20	2.4 ± 0.17	2.1–2.6
BRAZIL: Acre-3	21	2.3 ± 0.17	2.1–2.7
BRAZIL: Acre-4	5	2.3 ± 0.15	2.2–2.5
BRAZIL: Acre-5	7	2.3 ± 0.24	2.0–2.6
BRAZIL: Amazonas-1	15	2.3 ± 0.17	2.0–2.6
BRAZIL: Amazonas-2	17	2.3 ± 0.21	2.0–2.6
BRAZIL: Amazonas-3	29	2.3 ± 0.13	2.0–2.6
BRAZIL: Amazonas-4	18	2.3 ± 0.18	1.9–2.7
BRAZIL: Amazonas-5	35	2.4 ± 0.16	2.1–2.8
BRAZIL: Amazonas-6	26	2.4 ± 0.18	2.1–2.8
BRAZIL: Amazonas-7	24	2.4 ± 0.22	2.1–2.9
BRAZIL: Amazonas-8	13	2.4 ± 0.13	2.1–2.6
BRAZIL: Amazonas-9	2	2.2 ± 0.28	2.0–2.4
BRAZIL: Mato Grosso-2	26	2.2 ± 0.14	1.8–2.5
BRAZIL: Goiás	11	2.4 ± 0.14	2.2–2.6
BRAZIL: Federal District	10	2.3 ± 0.17	2.0–2.6
BRAZIL: Pará-1	29	2.5 ± 0.21	2.0–3.1
BRAZIL: Pará-2	16	2.5 ± 0.18	2.2–2.9
BRAZIL: Pará-3	9	2.4 ± 0.22	2.0–2.7
BRAZIL: Pará-4	36	2.2 ± 0.20	1.8–2.8
BRAZIL: Amapá	44	2.3 ± 0.17	2.0–2.7
PARAGUAY	13	2.4 ± 2.0	2.2–2.8
BRAZIL: Pernambuco	4	2.5 ± 0.38	2.0–2.8
BRAZIL: Bahia	3	2.6 ± 0.21	2.4–2.8
BRAZIL: Espírito Santo	3	2.3 ± 0.21	2.1–2.5
Crown length of M1–3			
FRENCH GUIANA	44	4.6 ± 0.16	4.2–5.0
SURINAM	7	4.5 ± 0.17	4.4–4.8
GUYANA: Barima-Waini	13	4.4 ± 0.15	4.2–4.7
GUYANA: Takutu-Essequibo	3	4.7 ± 0.21	4.5–4.9
VENEZUELA: Bolívar-1	32	4.9 ± 0.13	4.7–5.2
VENEZUELA: Bolívar-2	22	4.9 ± 0.16	4.6–5.2
VENEZUELA: Amazonas	9	4.9 ± 0.11	4.7–5.0
TRINIDAD	41	4.7 ± 0.14	4.5–5.0
COLOMBIA: Cundinamarca	23	5.1 ± 0.14	4.8–5.3
ECUADOR: Napo + Pastaza	35	5.1 ± 0.15	4.7–5.5
ECUADOR: Zamora-Chinchipe	2	5.0 ± 0.00	—
PERÚ: Loreto	2	5.0 ± 0.00	—
PERÚ: Pasco	21	5.2 ± 0.21	4.9–5.6
PERÚ: Junín (*perenensis*)	1	5.3	
PERÚ: Ucayali	21	5.0 ± 0.13	4.8–5.3
BOLIVIA: Pando-1	10	4.8 ± 0.19	4.5–5.1
BOLIVIA: Pando-2	1	4.8	
BOLIVIA: Beni	32	5.1 ± 0.12	4.7–5.3
BOLIVIA: Cochabamba	2	5.0 ± 0.07	4.9–5.0
BOLIVIA: Santa Cruz	10	5.0 ± 0.15	4.7–5.2
BRAZIL: Acre-1	5	5.0 ± 0.17	4.7–5.1
BRAZIL: Acre-2	20	5.0 ± 0.16	4.7–5.3
BRAZIL: Acre-3	21	5.0 ± 0.21	4.7–5.5
BRAZIL: Acre-4	5	5.0 ± 0.12	4.8–5.1
BRAZIL: Acre-5	7	5.0 ± 0.12	4.9–5.2
BRAZIL: Amazonas-1	15	5.0 ± 0.16	4.6–5.2
BRAZIL: Amazonas-2	17	5.1 ± 0.18	4.8–5.4
BRAZIL: Amazonas-3	29	5.0 ± 0.18	4.7–5.5
BRAZIL: Amazonas-4	18	4.9 ± 0.19	4.7–5.4
BRAZIL: Amazonas-5	35	5.1 ± 0.18	4.7–5.4
BRAZIL: Amazonas-6	26	5.0 ± 0.19	4.6–5.3
BRAZIL: Amazonas-7	24	5.0 ± 0.17	4.6–5.2
BRAZIL: Amazonas-8	13	5.0 ± 0.17	4.7–5.2
BRAZIL: Amazonas-9	2	4.8 ± 0.07	4.7–4.8
BRAZIL: Mato Grosso-2	26	4.6 ± 0.17	4.3–5.0
BRAZIL: Goiás	11	4.7 ± 0.16	4.4–4.9
BRAZIL: Federal District	10	4.9 ± 0.19	4.6–5.2
BRAZIL: Pará-1	29	4.9 ± 0.18	4.5–5.1
BRAZIL: Pará-2	16	4.7 ± 0.19	4.4–5.0
BRAZIL: Pará-3	9	4.7 ± 0.15	4.4–4.9
BRAZIL: Pará-4	36	4.3 ± 0.16	3.7–4.7
BRAZIL: Amapá	44	4.6 ± 0.15	4.2–4.9
PARAGUAY	13	4.7 ± 0.15	4.4–4.9
BRAZIL: Pernambuco	4	5.1 ± 0.10	5.1–5.2
BRAZIL: Bahia	3	5.2 ± 0.10	5.1–5.3
BRAZIL: Espírito Santo	3	5.2 ± 0.20	5.0–5.4
Breadth of M1			
FRENCH GUIANA	44	1.4 ± 0.06	1.2–1.5
SURINAM	7	1.3 ± 0.05	1.3–1.4
GUYANA: Barima-Waini	13	1.3 ± 0.08	1.2–1.4
GUYANA: Takutu-Essequibo	3	1.4 ± 0.06	1.3–1.4
VENEZUELA: Bolívar-1	32	1.4 ± 0.08	1.3–1.6
VENEZUELA: Bolívar-2	22	1.4 ± 0.08	1.3–1.5
VENEZUELA: Amazonas	9	1.4 ± 0.04	1.3–1.4
TRINIDAD	41	1.4 ± 0.06	1.3–1.5
COLOMBIA: Cundinamarca	23	1.5 ± 0.06	1.4–1.6
ECUADOR: Napo + Pastaza	35	1.5 ± 0.08	1.3–1.7
ECUADOR: Zamora-Chinchipe	2	1.5 ± 0.00	—
PERÚ: Loreto	2	1.5 ± 0.06	1.4–1.5
PERÚ: Pasco	21	1.6 ± 0.08	1.4–1.7
PERÚ: Junín (*perenensis*)	1	1.5	
PERÚ: Ucayali	21	1.4 ± 0.05	1.4–1.5

Sample	*N*	Mean ± SD	Observed range
BOLIVIA: Pando-1	10	1.4 ± 0.08	1.3–1.6
BOLIVIA: Pando-2	1	1.4	
BOLIVIA: Beni	32	1.5 ± 0.06	1.3–1.6
BOLIVIA: Cochabamba	2	1.5 ± 0.07	1.4–1.5
BOLIVIA: Santa Cruz	10	1.5 ± 0.04	1.4–1.5
BRAZIL: Acre-1	5	1.5 ± 0.06	1.4–1.5
BRAZIL: Acre-2	20	1.5 ± 0.07	1.4–1.6
BRAZIL: Acre-3	21	1.5 ± 0.05	1.4–1.6
BRAZIL: Acre-4	5	1.5 ± 0.05	1.4–1.5
BRAZIL: Acre-5	7	1.5 ± 0.05	1.4–1.5
BRAZIL: Amazonas-1	15	1.5 ± 0.08	1.3–1.6
BRAZIL: Amazonas-2	17	1.5 ± 0.07	1.4–1.6
BRAZIL: Amazonas-3	29	1.5 ± 0.06	1.4–1.6
BRAZIL: Amazonas-4	18	1.5 ± 0.07	1.4–1.6
BRAZIL: Amazonas-5	35	1.4 ± 0.06	1.4–1.6
BRAZIL: Amazonas-6	26	1.4 ± 0.06	1.3–1.5
BRAZIL: Amazonas-7	24	1.4 ± 0.05	1.4–1.5
BRAZIL: Amazonas-8	13	1.4 ± 0.07	1.3–1.5
BRAZIL: Amazonas-9	2	1.4 ± 0.00	—
BRAZIL: Mato Grosso-2	26	1.3 ± 0.06	1.2–1.6
BRAZIL: Goiás	11	1.4 ± 0.07	1.3–1.5
BRAZIL: Federal District	10	1.5 ± 0.06	1.4–1.6
BRAZIL: Pará-1	29	1.4 ± 0.07	1.3–1.5
BRAZIL: Pará-2	16	1.4 ± 0.07	1.3–1.5
BRAZIL: Pará-3	9	1.4 ± 0.10	1.3–1.5
BRAZIL: Pará-4	36	1.3 ± 0.06	1.1–1.4
BRAZIL: Amapá	44	1.3 ± 0.07	1.2–1.5
PARAGUAY	13	1.4 ± 0.05	1.4–1.5
BRAZIL: Pernambuco	4	1.5 ± 0.06	1.4–1.6
BRAZIL: Bahia	3	1.6 ± 0.06	1.5–1.6
BRAZIL: Espírito Santo	3	1.6 ± 0.06	1.5–1.6

APPENDIX B

List of Measured Specimens of the *Oryzomys megacephalus* Complex

Below we list the adults measured of *Oryzomys megacephalus* and *O. laticeps*. These specimens constitute the geographic samples from which the descriptive statistics listed in appendix A and multivariate statistical analyses were derived. Each sample is identified by number and name that corresponds to the numbered samples described in table 1.

1. **FRENCH GUIANA**
AMNH 266494, 266508, 266514, 266518, 266519, 266521, 266527, 266530, 266533, 266534, 266538, 266541, 267016, 267018; MNHN 1981-182, 1983-368–1983-370, 1986-289–1986-291, 1986-293, 1986-295, 1986-296, 1986-300, 1986-301, 1986-314, 1986-385, 1986-486–1986-488, 1986-492, 1986-493, 1986-497–1986-501, 1986-506, 1986-509, 1986-520, 1986-521, 1986-524, 1986-525
2. **SURINAM**
CM 76932, 76934, 76935; FMNH 93285, 93287–93289
3. **GUYANA: Barima-Waini**
ROM 98739, 98751, 98752, 98827, 98838, 98867, 98870, 98905, 98907, 98908, 100976, 101072, 101113
4. **GUYANA: Upper Takutu-Upper Essequibo**
ROM 97979, 98089, 98090
5. **VENEZUELA: Bolívar-1**
AMNH 130893, 130894, 130897, 130900, 130909, 130910, 130912, 130917, 130919, 130922, 130930, 130938, 130945, 130953, 130954, 130957, 130964, 130966, 130969, 130972, 130973, 130977–130982, 130985, 131021, 131099, 131123, 131134
6. **VENEZUELA: Bolívar-2**
AMNH 75756, 75758, 75760–75764, 75766–75769, 75771–75774, 75776, 75780, 75782, 75783, 75786, 75787, 75789
7. **VENEZUELA: Amazonas**
AMNH 77321, 78061–78064, 78067, 78068, 78075, 78077
8. **TRINIDAD**
AMNH 5949/4679 (holotype of *O. velutinus*), 174013, 174014, 174063, 186492, 186497–186499, 186503, 186504, 186508, 186511, 186515, 186517, 186522, 186532, 186536, 186538, 186543, 186544, 186549, 188426–188428, 188433, 188439, 188441, 188444, 188456, 188457, 188463, 188465, 188467, 188469, 188472, 188474, 189325, 189344, 189350, 208781, 208782
9. **COLOMBIA: Cundinamarca**
AMNH 70526, 71297, 71298, 71300, 71306, 71312–71314, 71316–71319, 71321–71325, 71327, 71331, 71338, 76720; USNM 251964, 251966
10. **ECUADOR: Napo + Pastaza**
AMNH 67352, 67400, 68048, 68051, 68060, 68072, 68074, 68075, 68079, 68081, 68084–68088, 68093, 68095–68097, 68099–68101, 68104, 68107, 68111, 68113, 68114, 68116, 68117; USNM 267501, 513540–513542, 528353, 528355
11. **ECUADOR: Zamora-Chinchipe**
AMNH 36577, 47822
12. **PERÚ: Loreto**
BMNH 54.423, 54.424
13. **PERÚ: Pasco**
AMNH 213503, 230943, 230944, 230946–230948, 230951–230953, 230955, 230956, 230958, 230965–230967, 230970–230973, 230975, 230976
14. **PERÚ: Junín**
BMNH 0.7.7.25 (holotype of *O. perenensis*)
15. **PERÚ: Ucayali**
LSUMZ 12319, 12348, 12350–12352, 12356, 14358, 14359, 16680, 16682–16684, 16692; MVZ 136575, 136577, 136579, 136580, 136582–136584, 136586, 136589
16. **BOLIVIA: Pando-1**
AMNH 262937, 262939–262944, 262946, 262947, 262966
17. **BOLIVIA: Pando-2**
AMNH 262936
18. **BOLIVIA: Beni**
AMNH 209966, 209970, 209974, 209979, 209980, 209983, 209988–209991, 209950, 209951, 209953, 209955, 209957, 209958, 209961, 209964, 209992, 209999, 210002, 210003, 210005, 210016, 210017, 210019–210021, 210357, 210361, 246139, 246140
19. **BOLIVIA: Cochabamba**
AMNH 247778, 247780
20. **BOLIVIA: Santa Cruz**
AMNH 211740, 211744, 262015, 262021, 262041, 262080, 262084–262086, 263880
21. **BRAZIL: Acre-1**
USNM 545295, 545298, 545299, 545303, 545305
22. **BRAZIL: Acre-2**
MNFS 1241–1244, 1246, 1334, 1335, 1340, 1341–1343, 1346, 1348, 1374, 1388, 1390, 1391, 1405, 1407, 1408

23. **BRAZIL: Acre-3**
MNFS 1100, 1116, 1120, 1144–1146, 1148, 1149, 1168, 1169, 1170, 1173, 1204–1206, 1227, 1268, 1330, 1400, 1418, 1423
24. **BRAZIL: Acre-4**
JUR 216, 219, 246; MNFS 1464, 1566
25. **BRAZIL: Acre-5**
JUR 228, 237; MNFS 1586, 1587, 1612–1614
26. **BRAZIL: Amazonas-1**
JLP 15529, 15536, 15564, 15604, 15609, 15646, 15650, 15687–15689, 15694, 15706, 15707, 15719, 15740
27. **BRAZIL: Amazonas-2**
JUR 162, 163, 174, 175; MNFS 586–588, 621, 630, 631, 633, 634, 643–646, 657
28. **BRAZIL: Amazonas-3**
JLP 15229, 15242, 15248, 15249, 15256, 15259, 15272, 15274, 15291, 15311, 15322, 15330–15332, 15362, 15456, 15499, 15507; MNFS 329, 330, 385, 389, 404, 405, 420, 421, 498, 510, 520
29. **BRAZIL: Amazonas-4**
JLP 15417, 15418, 15447: JUR 1, 4, 6, 10, 12, 14, 36, 39, 40, 42, 43, 47, 76, 77, 79
30. **BRAZIL: Amazonas-5**
JLP 15748, 15762, 15763, 15768–15772, 15782, 15790, 15813, 15865, 15871, 15875–15877, 15881, 15883, 15892, 15901, 16030; MNFS 682, 685, 686, 736–738, 750, 761, 827, 828, 868, 917, 952, 954
31. **BRAZIL: Amazonas-6**
JLP 15822, 15823, 15825, 15967, 15968, 16026, 16027, 16067; MNFS 693, 694, 696, 699, 705, 706, 712, 713, 716, 751, 765, 767, 777, 779, 786, 787, 897
32. **BRAZIL: Amazonas-7**
JUR 422, 424, 427, 441–444, 454, 455, 465, 491, 493, 514–516, 522, 523, 531, 554, 556, 558, 561, 564, 568
33. **BRAZIL: Amazonas-8**
JUR 510–513, 526–530, 537, 538, 555; MNFS 1786
34. **BRAZIL: Amazonas-9**
USNM 580002, 580003
35. **BRAZIL: Mato Grosso-2**
BMNH 81.550–81.553, 81.555–81.562, 81.564–81.567, 86.1130, 86.1131, 86.1135, 86.1137, 86.1139–86.1142, 86.1144, 86.1145
36. **BRAZIL: Goiás**
AMNH 134565, 134570, 134572, 134573, 134575, 134579, 134583, 134584, 134590, 134774, 202663
37. **BRAZIL: Federal District**
OMNH 17459, 17460, 17462, 17464, 17466–17468, 17472–17474
38. **BRAZIL: Pará-1**
USNM 461934–461944, 545255–545262, 545264, 545266–545274
39. **BRAZIL: Pará-2**
USNM 461740–461751, 543342, 544624, 544626; BMNH 97.4.1.1 (holotype of *O. goeldi*)
40. **BRAZIL: Pará-3**
USNM 521443, 521446, 521450, 521451, 521520, 521522–521525
41. **BRAZIL: Pará-4**
AMNH 95989, 95990, 95992, 95994, 95995, 95998, 95999, 96003, 96005, 96779–96783, 96786, 96788–96792, 96794–96796, 188965, 188966, 203379, 203380, 203382, 203384–203387, 203389, 203390, 203393, 203395
44. **BRAZIL: Amapá**
USNM 393950, 393954, 393958, 393964, 393966, 393968, 393970, 393971, 393975, 393977, 393984, 393991–393993, 393995, 393996, 394002–394004, 394007, 394008, 394010, 394053, 394055–394057, 394060, 394061, 394063, 394065, 394066, 394070, 394072, 394077, 394079, 394082, 394084, 394086, 394091, 394093, 394100, 394104, 394110, 394112
45. **PARAGUAY**
UMMZ 125454, 125291, 126010, 133801–133804, 133807, 133808, 133811, 137010–137012
46. **BRAZIL: Pernambuco**
BMNH 3.10.1.42 (holotype of *O. oniscus*), 3.10.1.43, 3.10.1.46, 3.10.1.47
47. **BRAZIL: Bahia**
USNM 304571, 545055, 545056
48. **BRAZIL: Espírito Santo**
USNM 62903, 62904, 62906

APPENDIX C

Descriptive Statistics for Cranial and Dental Measurements (mm) for Samples of the *Oryzomys yunganus* Group

Samples are from throughout the geographic range and consist of specimens from one or more localities, which are identified in table 16. Only adults (young to old) were measured, which are identified in appendix D.

Sample	*N*	Mean ± SD	Observed range
Occipitonasal length			
FRENCH GUIANA	18	29.9 ± 0.84	28.4–31.1
SURINAM	10	30.4 ± 0.82	29.1–31.5
GUYANA	7	29.9 ± 1.28	27.8–31.5
VENEZUELA: Bolívar	14	31.5 ± 0.98	29.5–33.2
COLOMBIA: Central	6	32.8 ± 0.94	30.5–33.1
ECUADOR: Napo + E Pastaza	7	32.4 ± 1.30	31.4–35.1
ECUADOR: Tung. + W Pastaza	12	32.7 ± 0.90	30.9–33.9
PERÚ: Northern	16	33.2 ± 1.60	29.4–34.5
PERÚ: Central	9	31.4 ± 0.96	30.4–33.0
PERÚ: Southern	13	32.5 ± 1.24	30.9–35.3
BOLIVIA: Pando + Beni	5	28.7 ± 0.89	27.8–30.1
BOLIVIA: Santa Cruz	3	30.5 ± 0.82	29.8–31.4
PERÚ + BRAZIL	8	31.2 ± 1.76	28.8–34.8
BRAZIL: Acre	11	31.6 ± 1.03	29.9–32.9
BRAZIL: Amazonas-1	15	31.8 ± 1.22	29.9–33.4
BRAZIL: Amazonas-2	38	30.8 ± 1.03	28.9–32.9
BRAZIL: Amazonas-3	4	30.8 ± 0.59	30.0–31.3
BRAZIL: Mato Grosso	33	29.4 ± 0.87	27.5–31.4
BRAZIL: Pará	5	29.9 ± 1.01	28.9–31.2
BRAZIL: Amapá	29	29.9 ± 0.97	28.2–31.6
Zygomatic breadth			
FRENCH GUIANA	18	14.6 ± 0.65	13.3–15.8
SURINAM	10	15.0 ± 0.40	14.5–15.7
GUYANA	7	15.2 ± 0.51	14.3–15.7
VENEZUELA: Bolívar	14	15.8 ± 0.56	14.8–16.9
COLOMBIA: Central	6	16.2 ± 0.61	15.3–16.9
ECUADOR: Napo + E Pastaza	7	16.5 ± 0.55	15.9–17.3
ECUADOR: Tung. + W Pastaza	12	16.8 ± 0.47	16.3–17.6
PERÚ: Northern	16	16.0 ± 0.67	15.2–17.3
PERÚ: Central	9	15.7 ± 0.71	14.2–16.4
PERÚ: Southern	13	16.7 ± 0.47	16.1–17.6
BOLIVIA: Pando + Beni	5	14.8 ± 0.68	14.0–15.8
BOLIVIA: Santa Cruz	3	15.9 ± 0.55	15.5–16.5
PERÚ + BRAZIL	8	16.1 ± 0.74	15.3–17.7
BRAZIL: Acre	11	16.2 ± 0.46	15.6–17.0
BRAZIL: Amazonas-1	15	16.3 ± 0.66	15.2–17.4
BRAZIL: Amazonas-2	38	15.8 ± 0.45	15.0–16.7
BRAZIL: Amazonas-3	4	15.5 ± 0.22	15.3–15.8
BRAZIL: Mato Grosso	33	14.8 ± 0.38	14.0–15.5
BRAZIL: Pará	5	14.9 ± 0.56	14.0–15.4
BRAZIL: Amapá	29	14.7 ± 0.57	13.5–15.3
Interorbital breadth			
FRENCH GUIANA	18	5.0 ± 0.14	4.8–5.3
SURINAM	10	5.0 ± 0.16	4.8–5.3
GUYANA	7	5.0 ± 0.18	4.8–5.3
VENEZUELA: Bolívar	14	5.2 ± 0.16	4.9–5.5
COLOMBIA: Central	6	5.0 ± 0.14	4.8–5.2
ECUADOR: Napo + E Pastaza	7	5.1 ± 0.28	4.8–5.7
ECUADOR: Tung. + W Pastaza	13	5.4 ± 0.12	5.2–5.6
PERÚ: Northern	16	5.3 ± 0.22	5.0–5.7
PERÚ: Central	9	5.2 ± 0.17	5.0–5.5
PERÚ: Southern	12	5.2 ± 0.25	4.6–5.6
BOLIVIA: Pando + Beni	5	5.0 ± 0.18	4.7–5.2
BOLIVIA: Santa Cruz	3	5.2 ± 0.10	5.1–5.3
PERÚ + BRAZIL	8	5.1 ± 0.19	4.8–5.4
BRAZIL: Acre	11	5.1 ± 0.14	4.9–5.4
BRAZIL: Amazonas-1	15	5.1 ± 0.17	4.7–5.4
BRAZIL: Amazonas-2	38	5.1 ± 0.16	4.7–5.5
BRAZIL: Amazonas-3	4	5.0 ± 0.14	4.9–5.2
BRAZIL: Mato Grosso	33	4.8 ± 0.14	4.5–5.1
BRAZIL: Pará	5	5.0 ± 0.14	4.8–5.2
BRAZIL: Amapá	29	5.0 ± 0.15	4.7–5.3
Length of rostrum			
FRENCH GUIANA	18	9.3 ± 0.43	8.7–10.0
SURINAM	10	9.4 ± 0.36	8.8–9.8
GUYANA	7	9.3 ± 0.64	8.4–10.4
VENEZUELA: Bolívar	14	9.6 ± 0.34	8.8–10.3
COLOMBIA: Central	6	9.7 ± 0.16	9.6–10.0
ECUADOR: Napo + E Pastaza	7	9.9 ± 0.69	9.4–11.3
ECUADOR: Tung. + W Pastaza	12	10.3 ± 0.52	9.3–11.1
PERÚ: Northern	16	9.7 ± 0.59	9.0–11.6
PERÚ: Central	9	9.7 ± 0.32	9.0–10.0
PERÚ: Southern	13	10.0 ± 0.53	9.0–11.0
BOLIVIA: Pando + Beni	5	8.7 ± 0.38	8.4–9.3
BOLIVIA: Santa Cruz	3	9.5 ± 0.45	9.0–9.9
PERÚ + BRAZIL	8	9.8 ± 0.81	8.9–11.1
BRAZIL: Acre	11	9.6 ± 0.44	8.7–10.1
BRAZIL: Amazonas-1	15	9.8 ± 0.56	8.7–10.7

Sample	*N*	Mean ± SD	Observed range
BRAZIL: Amazonas-2	38	9.4 ± 0.50	8.5–10.6
BRAZIL: Amazonas-3	4	9.6 ± 0.29	9.3–10.0
BRAZIL: Mato Grosso	33	9.1 ± 0.42	8.2–9.9
BRAZIL: Pará	5	9.2 ± 0.57	8.7–9.9
BRAZIL: Amapá	29	9.3 ± 0.41	8.6–10.0
Breadth of rostrum			
FRENCH GUIANA	18	5.9 ± 0.35	5.1–6.5
SURINAM	10	6.1 ± 0.30	5.7–6.5
GUYANA	7	5.8 ± 0.38	5.1–6.2
VENEZUELA: Bolívar	14	6.3 ± 0.35	5.7–6.9
COLOMBIA: Central	6	6.0 ± 0.33	5.5–6.4
ECUADOR: Napo + E Pastaza	7	6.1 ± 0.29	5.7–6.5
ECUADOR: Tung. + W Pastaza	12	6.2 ± 0.52	5.5–7.3
PERÚ: Northern	16	5.8 ± 0.44	5.4–7.2
PERÚ: Central	9	6.2 ± 0.43	5.6–7.0
PERÚ: Southern	13	6.2 ± 0.31	5.8–6.9
BOLIVIA: Pando + Beni	5	5.5 ± 0.36	5.0–6.0
BOLIVIA: Santa Cruz	3	6.2 ± 0.15	6.1–6.4
PERÚ + BRAZIL	8	6.1 ± 0.35	5.7–6.6
BRAZIL: Acre	11	6.1 ± 0.33	5.6–6.6
BRAZIL: Amazonas-1	15	6.1 ± 0.46	5.1–6.8
BRAZIL: Amazonas-2	38	5.8 ± 0.38	5.0–6.7
BRAZIL: Amazonas-3	4	6.0 ± 0.06	5.9–6.0
BRAZIL: Mato Grosso	33	5.6 ± 0.30	5.1–6.6
BRAZIL: Pará	5	6.0 ± 0.26	5.5–6.1
BRAZIL: Amapá	29	5.8 ± 0.37	5.1–6.6
Lambdoidal breadth			
FRENCH GUIANA	18	11.3 ± 0.34	10.6–12.0
SURINAM	10	11.6 ± 0.26	11.2–12.0
GUYANA	7	11.6 ± 0.29	11.1–12.0
VENEZUELA: Bolívar	14	11.9 ± 0.34	11.3–12.4
COLOMBIA: Central	6	11.8 ± 0.34	11.5–12.1
ECUADOR: Napo + E Pastaza	7	11.9 ± 0.54	11.4–12.9
ECUADOR: Tung. + W Pastaza	12	12.3 ± 0.26	11.9–12.8
PERÚ: Northern	16	12.0 ± 0.42	11.5–13.0
PERÚ: Central	9	12.0 ± 0.30	11.5–12.5
PERÚ: Southern	13	12.2 ± 0.51	11.5–13.2
BOLIVIA: Pando + Beni	5	11.3 ± 0.50	10.6–12.0
BOLIVIA: Santa Cruz	3	11.8 ± 0.25	11.6–12.1
PERÚ + BRAZIL	8	12.1 ± 0.42	11.4–12.9
BRAZIL: Acre	11	12.0 ± 0.36	11.6–12.7
BRAZIL: Amazonas-1	15	12.2 ± 0.39	11.7–13.0
BRAZIL: Amazonas-2	38	11.9 ± 0.35	11.3–12.7
BRAZIL: Amazonas-3	4	11.6 ± 0.05	11.6–11.7
BRAZIL: Mato Grosso	33	11.2 ± 0.36	10.4–12.2
BRAZIL: Pará	5	11.3 ± 0.34	10.8–11.7
BRAZIL: Amapá	29	11.3 ± 0.30	10.8–11.9

Sample	*N*	Mean ± SD	Observed range
Height of braincase			
FRENCH GUIANA	18	8.3 ± 0.35	7.5–9.0
SURINAM	10	8.3 ± 0.24	8.0–8.7
GUYANA	7	8.5 ± 0.19	8.3–8.9
VENEZUELA: Bolívar	14	8.7 ± 0.33	8.1–9.3
COLOMBIA: Central	6	8.4 ± 0.31	8.0–8.8
ECUADOR: Napo + E Pastaza	7	8.7 ± 0.33	8.3–9.2
ECUADOR: Tung. + W Pastaza	12	8.8 ± 0.41	8.1–9.2
PERÚ: Northern	16	8.5 ± 0.34	8.1–9.6
PERÚ: Central	9	8.6 ± 0.25	8.1–8.9
PERÚ: Southern	13	8.5 ± 0.36	7.7–9.1
BOLIVIA: Pando + Beni	5	8.4 ± 0.22	8.1–8.7
BOLIVIA: Santa Cruz	3	8.5 ± 0.23	8.2–8.6
PERÚ + BRAZIL	8	8.5 ± 0.37	8.0–9.1
BRAZIL: Acre	11	8.7 ± 0.42	8.0–9.2
BRAZIL: Amazonas-1	15	8.7 ± 0.28	8.3–9.2
BRAZIL: Amazonas-2	38	8.6 ± 0.26	7.9–9.2
BRAZIL: Amazonas-3	4	8.2 ± 0.35	7.8–8.6
BRAZIL: Mato Grosso	33	8.3 ± 0.25	7.8–8.9
BRAZIL: Pará	5	8.1 ± 0.27	7.8–8.4
BRAZIL: Amapá	29	8.1 ± 0.35	7.5–8.9
Breadth of zygomatic plate			
FRENCH GUIANA	18	3.5 ± 0.29	3.0–4.0
SURINAM	10	3.3 ± 0.11	3.2–3.5
GUYANA	7	3.3 ± 0.21	3.0–3.6
VENEZUELA: Bolívar	14	4.0 ± 0.30	3.3–4.5
COLOMBIA: Central	6	3.6 ± 0.32	3.2–3.9
ECUADOR: Napo + E Pastaza	7	3.8 ± 0.19	3.5–4.1
ECUADOR: Tung. + W Pastaza	12	4.1 ± 0.19	3.8–4.5
PERÚ: Northern	16	3.6 ± 0.28	3.2–4.1
PERÚ: Central	9	3.6 ± 0.19	3.3–3.9
PERÚ: Southern	13	3.7 ± 0.16	3.4–4.0
BOLIVIA: Pando + Beni	5	3.4 ± 0.22	3.1–3.7
BOLIVIA: Santa Cruz	3	3.3 ± 0.06	3.2–3.3
PERÚ + BRAZIL	8	3.6 ± 0.36	3.0–4.2
BRAZIL: Acre	11	3.7 ± 0.21	3.3–4.0
BRAZIL: Amazonas-1	15	3.8 ± 0.17	3.5–4.2
BRAZIL: Amazonas-2	38	3.6 ± 0.24	3.1–4.2
BRAZIL: Amazonas-3	4	3.5 ± 0.28	3.2–3.8
BRAZIL: Mato Grosso	33	3.4 ± 0.18	3.0–3.9
BRAZIL: Pará	5	3.3 ± 0.16	3.0–3.4
BRAZIL: Amapá	29	3.5 ± 0.21	3.1–4.1
Length of diastema			
FRENCH GUIANA	18	7.8 ± 0.31	7.2–8.3
SURINAM	10	7.8 ± 0.54	6.8–8.6
GUYANA	7	7.7 ± 0.40	7.0–8.2
VENEZUELA: Bolívar	14	8.0 ± 0.33	7.4–8.6
COLOMBIA: Central	6	7.8 ± 0.56	7.2–8.5

Sample	N	Mean ± SD	Observed range
ECUADOR: Napo + E Pastaza	7	8.1 ± 0.65	7.4–9.1
ECUADOR: Tung. + W Pastaza	12	7.9 ± 0.29	7.5–8.4
PERÚ: Northern	16	7.7 ± 0.61	7.0–8.9
PERÚ: Central	9	7.6 ± 0.46	7.0–8.3
PERÚ: Southern	13	8.0 ± 0.32	7.6–8.7
BOLIVIA: Pando + Beni	5	7.2 ± 0.39	6.8–7.8
BOLIVIA: Santa Cruz	3	7.4 ± 0.35	7.0–7.7
PERÚ + BRAZIL	8	7.7 ± 0.60	6.9–8.7
BRAZIL: Acre	11	8.1 ± 0.43	7.5–8.7
BRAZIL: Amazonas-1	15	8.1 ± 0.42	7.5–9.0
BRAZIL: Amazonas-2	38	7.8 ± 0.33	7.2–8.9
BRAZIL: Amazonas-3	4	7.8 ± 0.15	7.6–9.0
BRAZIL: Mato Grosso	33	7.3 ± 0.37	6.7–8.1
BRAZIL: Pará	5	7.4 ± 0.25	7.1–7.7
BRAZIL: Amapá	29	7.7 ± 0.38	6.9–8.4

Length of bony palate

Sample	N	Mean ± SD	Observed range
FRENCH GUIANA	18	6.6 ± 0.27	6.0–6.9
SURINAM	10	6.7 ± 0.29	6.2–7.2
GUYANA	7	6.4 ± 0.32	5.7–6.7
VENEZUELA: Bolívar	14	7.4 ± 0.37	6.8–8.3
COLOMBIA: Central	6	7.0 ± 0.14	6.8–7.2
ECUADOR: Napo + E Pastaza	7	7.0 ± 0.38	6.4–7.5
ECUADOR: Tung. + W Pastaza	12	7.5 ± 0.28	7.1–8.2
PERÚ: Northern	16	6.7 ± 0.28	6.2–7.1
PERÚ: Central	9	6.7 ± 0.37	6.3–7.3
PERÚ: Southern	13	7.1 ± 0.42	6.4–7.8
BOLIVIA: Pando + Beni	5	6.2 ± 0.14	6.1–6.4
BOLIVIA: Santa Cruz	3	6.3 ± 0.17	6.2–6.5
PERÚ + BRAZIL	8	6.7 ± 0.56	5.6–7.3
BRAZIL: Acre	11	7.0 ± 0.52	6.2–8.1
BRAZIL: Amazonas-1	15	7.0 ± 0.25	6.6–7.5
BRAZIL: Amazonas-2	38	6.9 ± 0.38	6.0–7.0
BRAZIL: Amazonas-3	4	6.9 ± 0.20	6.8–7.2
BRAZIL: Mato Grosso	33	6.4 ± 0.20	6.1–7.0
BRAZIL: Pará	5	6.6 ± 0.33	6.3–7.0
BRAZIL: Amapá	29	6.8 ± 0.54	6.0–7.9

Postpalatal length

Sample	N	Mean ± SD	Observed range
FRENCH GUIANA	18	9.8 ± 0.39	9.0–10.5
SURINAM	10	10.0 ± 0.52	9.3–11.0
GUYANA	7	10.0 ± 0.69	9.0–11.1
VENEZUELA: Bolívar	14	10.6 ± 0.53	9.2–11.2
COLOMBIA: Central	6	10.5 ± 0.53	9.6–11.1
ECUADOR: Napo + E Pastaza	7	10.9 ± 0.61	10.3–11.9
ECUADOR: Tung. + W Pastaza	12	10.6 ± 0.65	9.4–11.9
PERÚ: Northern	16	10.2 ± 0.77	9.0–11.8
PERÚ: Central	9	10.6 ± 0.73	9.7–12.1
PERÚ: Southern	13	10.7 ± 0.51	9.8–11.5
BOLIVIA: Pando + Beni	5	9.5 ± 0.42	9.0–10.1
BOLIVIA: Santa Cruz	3	10.5 ± 0.12	10.4–10.6
PERÚ + BRAZIL	8	10.2 ± 0.72	9.4–11.5
BRAZIL: Acre	11	10.6 ± 0.47	10.0–11.5
BRAZIL: Amazonas-1	15	10.6 ± 0.66	9.6–11.8
BRAZIL: Amazonas-2	38	10.2 ±0.39	9.3–11.0
BRAZIL: Amazonas-3	4	10.4 ± 0.34	10.1–10.8
BRAZIL: Mato Grosso	33	9.7 ± 0.44	8.9–10.9
BRAZIL: Pará	5	9.6 ± 0.16	9.4–9.8
BRAZIL: Amapá	29	9.6 ± 0.46	8.8–10.4

Length of incisive foramina

Sample	N	Mean ± SD	Observed range
FRENCH GUIANA	18	4.4 ± 0.22	4.0–4.8
SURINAM	10	4.7 ± 0.34	4.3–5.3
GUYANA	7	4.4 ± 0.19	4.1–4.7
VENEZUELA: Bolívar	14	4.7 ± 0.26	4.1–5.0
COLOMBIA: Central	5	4.9 ± 0.36	4.4–5.4
ECUADOR: Napo + E Pastaza	7	5.1 ± 0.32	4.8–5.7
ECUADOR: Tung. + W Pastaza	12	4.5 ± 0.19	4.2–4.9
PERÚ: Northern	16	5.0 ± 0.46	4.3–5.8
PERÚ: Central	9	4.9 ± 0.46	4.2–5.5
PERÚ: Southern	13	5.1 ± 0.30	4.7–5.6
BOLIVIA: Pando	5	4.3 ± 0.30	4.0–4.8
BOLIVIA: Santa Cruz	3	4.7 ± 0.42	4.2–5.0
PERÚ + BRAZIL	8	4.7 ± 0.46	3.9–5.5
BRAZIL: Acre	11	4.5 ± 0.29	4.0–4.9
BRAZIL: Amazonas-1	15	4.6 ± 0.34	4.0–5.1
BRAZIL: Amazonas-2	38	4.6 ± 0.26	4.1–5.3
BRAZIL: Amazonas-3	4	4.4 ± 0.17	4.1–4.5
BRAZIL: Mato Grosso	33	4.6 ± 0.28	4.0–5.4
BRAZIL: Pará	5	4.6 ± 0.24	4.4–5.0
BRAZIL: Amapá	29	4.6 ± 0.28	4.0–5.1

Breadth of incisive foramina

Sample	N	Mean ± SD	Observed range
FRENCH GUIANA	18	2.0 ± 0.12	1.8–2.2
SURINAM	10	2.2 ± 0.14	2.0–2.4
GUYANA	7	2.1 ± 0.15	1.9–2.3
VENEZUELA: Bolívar	14	2.3 ± 0.13	2.0–2.5
COLOMBIA: Central	6	2.4 ± 0.18	2.1–2.6
ECUADOR: Napo + E Pastaza	7	2.4 ± 0.14	2.3–2.6
ECUADOR: Tung. + W Pastaza	12	2.2 ± 0.14	1.9–2.4
PERÚ: Northern	16	2.4 ± 0.13	2.2–2.6
PERÚ: Central	9	2.2 ± 0.25	1.7–2.5
PERÚ: Southern	13	2.3 ± 0.21	1.9–2.7
BOLIVIA: Pando	5	2.1 ± 0.24	1.9–2.4
BOLIVIA: Santa Cruz	3	2.5 ± 0.06	2.5–2.6
PERÚ + BRAZIL	8	2.2 ± 0.20	1.9–2.4
BRAZIL: Acre	11	2.3 ± 0.13	2.1–2.5
BRAZIL: Amazonas-1	15	2.3 ± 0.16	2.0–2.6

Sample	*N*	Mean ± SD	Observed range
BRAZIL: Amazonas-2	38	2.3 ± 0.12	2.0–2.5
BRAZIL: Amazonas-3	4	2.3 ± 0.18	2.1–2.5
BRAZIL: Mato Grosso	33	2.2 ± 0.15	1.9–2.5
BRAZIL: Pará	5	2.2 ± 0.17	1.9–2.3
BRAZIL: Amapá	29	2.2 ± 0.17	1.9–2.5
Crown length of M1–3			
FRENCH GUIANA	18	4.3 ± 0.22	3.9–4.7
SURINAM	10	4.5 ± 0.15	4.2–4.7
GUYANA	7	4.3 ± 0.11	4.2–4.5
VENEZUELA: Bolívar	14	5.0 ± 0.14	4.8–5.3
COLOMBIA: Central	6	5.1 ± 0.25	4.8–5.4
ECUADOR: Napo + E Pastaza	7	5.1 ± 0.14	4.9–5.3
ECUADOR: Tung. + W Pastaza	12	5.6 ± 0.17	5.5–5.7
PERÚ: Northern	16	5.1 ± 0.15	4.8–5.3
PERÚ: Central	9	5.1 ± 0.15	4.9–5.3
PERÚ: Southern	13	5.1 ± 0.19	4.8–5.5
BOLIVIA: Pando	5	4.7 ± 0.12	4.5–4.8
BOLIVIA: Santa Cruz	3	4.7 ± 0.06	4.7–4.8
PERÚ + BRAZIL	8	5.0 ± 0.18	4.6–5.2
BRAZIL: Acre	11	4.9 ± 0.18	4.6–5.2
BRAZIL: Amazonas-1	15	4.7 ± 0.14	4.5–5.0
BRAZIL: Amazonas-2	38	4.8 ± 0.15	4.5–5.1
BRAZIL: Amazonas-3	4	4.7 ± 0.96	4.6–4.8
BRAZIL: Mato Grosso	33	4.6 ± 0.12	4.3–4.8
BRAZIL: Pará	5	4.6 ± 0.13	4.5–4.8
BRAZIL: Amapá	29	4.5 ± 0.13	4.3–4.8
Breadth of M1			
FRENCH GUIANA	18	1.4 ± 0.15	1.3–1.5
SURINAM	10	1.4 ± 0.03	1.3–1.4
GUYANA	7	1.4 ± 0.00	—
VENEZUELA: Bolívar	14	1.5 ± 0.04	1.5–1.6
COLOMBIA: Central	6	1.6 ± 0.08	1.5–1.7
ECUADOR: Napo + E Pastaza	7	1.6 ± 0.05	1.5–1.6
ECUADOR: Tung. + W Pastaza	12	1.8 ± 0.05	1.7–1.9
PERÚ: Northern	16	1.6 ± 0.07	1.5–1.7
PERÚ: Central	9	1.5 ± 0.04	1.5–1.6
PERÚ: Southern	13	1.5 ± 0.03	1.5–1.6
BOLIVIA: Pando	5	1.5 ± 0.00	—
BOLIVIA: Santa Cruz	3	1.4 ± 0.06	1.4–1.5
PERÚ + BRAZIL	8	1.5 ± 0.07	1.4–1.6
BRAZIL: Acre	11	1.5 ± 0.05	1.5–1.6
BRAZIL: Amazonas-1	15	1.5 ± 0.06	1.4–1.6
BRAZIL: Amazonas-2	38	1.5 ± 0.06	1.4–1.6
BRAZIL: Amazonas-3	4	1.5 ± 0.06	1.4–1.5
BRAZIL: Mato Grosso	33	1.4 ± 0.05	1.3–1.5
BRAZIL: Pará	5	1.4 ± 0.07	1.3–1.5
BRAZIL: Amapá	29	1.4 ± 0.07	1.3–1.5

APPENDIX D

List of Measured Specimens in Samples of the *Oryzomys yunganus* Group

Below we list specimens measured of *Oryzomys yunganus* and *O. tatei* (Tungurahua + W Pastaza). They form the geographic samples from which the descriptive statistics listed in appendix C and means used in cluster analyses were derived. Each sample is identified by name of country (or by country plus state or province) and is described in table 16.

FRENCH GUIANA
AMNH 266495, 266496, 266500, 266503, 266516, 266531, 267017; MNHN 1986-294, 1986-297, 1986-322, 1986-326, 1986-327, 1986-800–1986-803, 1986-881, 1986-883

SURINAM
CM 76926–76931, 76933, 76936, 76937; FMNH 93284

GUYANA
ROM 98719, 98738, 98747, 98771, 98782, 98824, 98826

VENEZUELA: Bolívar
AMNH 75770, 130898, 130901, 130905, 130906, 130914, 130916, 130933, 130940, 130955, 130959, 130960, 131125, 131126

COLOMBIA: Central
AMNH 71328, 136357; FMNH 58778, 58779, 87969, 87970

ECUADOR: Napo + E Pastaza
AMNH 68059, 68106; BMNH 54.432, 54.436; UMMZ 80095, 80106, 80108

ECUADOR: Tungurahua + W Pastaza
AMNH 67357–67360, 67361 (holotype of *O. tatei*), 67362–67367, 67376

PERÚ: Northern
BMNH 26.5.3.33, 26.5.3.34, 26.5.3.38–26.5.3.40, 26.5.3.42, 26.8.6.14–26.8.6.16, 54.421, 54.425, 54.426, 54.429, 54.430, 54.443; FMNH 19376

PERÚ: Central
BMNH 28.5.1.9, 28.5.1.13, 28.5.1.14; FMNH 23721, 24544, 24546–24548, 24551

PERÚ: Southern
FMNH 66399, 66401, 75253, 75254, 75257, 75259, 75261–75364, 75272; KU 144519, 144521

BOLIVIA: Pando + Beni
AMNH 262736, 262950–262952, 262957

BOLIVIA: Santa Cruz
AMNH 262079, 262081; MSB 56001

PERÚ + BRAZIL
LSUMZ 16685, 16687, 16689; MVZ 136585; USNM 545296, 545300, 545302, 545304

BRAZIL: Acre
JUR 214; MNFS 1004, 1128, 1171, 1172, 1181, 1240, 1323, 1347, 1455, 1588

BRAZIL: Amazonas-1
JLP 15257, 15415, 15446, 15535, 15605, 15720; JUR 2, 8, 35, 37, 38, 46, 75, 110; MNFS 527

BRAZIL: Amazonas-2
JLP 15262, 15263, 15265, 15275, 15281, 15283, 15288, 15289, 15312, 15319, 15321, 15324–15329, 15361, 15476, 15495, 15519, 15759, 16021, 16068; MNFS 335, 341, 349, 368, 384, 387, 388, 391, 392, 412, 511, 519, 521, 697

BRAZIL: Amazonas-3
JUR 464, 474, 524, 557

BRAZIL: Mato Grosso
BMNH 81.470, 81.472–81.474, 81.518, 81.521, 81.523, 81.534–81.541, 81.543–81.549, 81.554, 81.569, 81.572, 81.574, 81.576, 81.593, 86.1132–86.1134, 86.1138, 86.1147

BRAZIL: Pará
USNM 521444, 521445, 521519, 521521, 521527

BRAZIL: Amapá
USNM 393866, 393868, 393869, 393871, 393872, 393878, 393886, 393899, 393905, 393916, 393961, 393969, 393979, 394006, 394021, 394022, 394041–394044, 394052, 394074, 394105, 394106, 394108, 394148, 394162, 394167, 461525

APPENDIX E

Descriptive Statistics for Cranial and Dental Measurements (mm) of the *Oryzomys nitidus* Group

Each sample consists of young- to old-adult specimens (appendix F) from one or more localities as identified in table 39.

Sample	*N*	Mean ± SD	Observed range
Occipitonasal length			
O. macconnelli			
GUIANAS	17	32.8 ± 1.29	30.5–35.5
VENEZUELA: Bolívar	19	34.5 ± 1.00	32.4–36.0
ECUADOR + PERÚ	32	33.5 ± 1.25	31.0–35.7
PERÚ: Cuzco	10	34.0 ± 1.01	32.3–35.7
BRAZIL: Amazonas	12	34.3 ± 0.66	33.3–35.2
BRAZIL: W Pará	20	32.6 ± 1.26	30.2–32.6
BRAZIL: E Pará	20	33.1 ± 1.06	31.1–35.5
BRAZIL: Amapá	21	32.9 ± 1.28	31.2–36.2
O. nitidus			
PERÚ: Ucayali + Junín	22	35.4 ± 1.35	30.2–35.6
PERÚ: Madre de Dios	42	33.2 ± 1.13	31.4–35.7
BOLIVIA: Pando	11	33.4 ± 0.67	32.4–33.4
BOLIVIA: La Paz	48	33.8 ± 1.24	31.4–36.3
BOLIVIA: Beni	17	33.3 ± 0.90	32.0–34.8
BOLIVIA: Santa Cruz-1	26	32.8 ± 1.16	30.6–35.4
BOLIVIA: Santa Cruz-2	21	33.8 ± 1.10	31.6–35.5
BOLIVIA: Santa Cruz-3	21	33.3 ± 0.96	31.5–35.6
BOLIVIA: Santa Cruz-4	26	33.1 ± 1.12	31.1–36.0
O. emmonsae			
BRAZIL: Pará	14	32.9 ± 1.29	31.0–34.9
O. russatus			
BOLIVIA: Chuquisaca	15	35.1 ± 1.37	32.6–37.7
BOLIVIA: Tarija	11	34.7 ± 1.21	32.2–34.7
ARGENTINA: Salta + Jujuy	14	34.5 ± 0.57	33.7–35.6
BRAZIL: São Paulo	38	35.3 ± 1.15	33.2–37.7
BRAZIL: ES + MG	12	35.3 ± 0.82	33.8–36.4
BRAZIL: MG + Goiás	13	36.7 ± 0.95	35.2–38.0
Zygomatic breadth			
O. macconnelli			
GUIANAS	17	15.6 ± 0.66	14.5–17.0
VENEZUELA: Bolívar	19	16.9 ± 0.59	15.5–17.7
ECUADOR + PERÚ	32	16.4 ± 0.63	15.1–18.0
PERÚ: Cuzco	10	16.6 ± 0.46	16.0–17.3
BRAZIL: Amazonas	12	16.8 ± 0.43	16.1–17.4
BRAZIL: W Pará	20	16.5 ± 0.75	15.1–18.5
BRAZIL: E Pará	20	15.7 ± 0.41	14.7–16.3
BRAZIL: Amapá	21	15.9 ± 0.70	14.4–17.0
O. nitidus			
PERÚ: Ucayali + Junín	22	16.9 ± 0.72	15.1–18.1
PERÚ: Madre de Dios	42	16.9 ± 0.74	15.1–18.3
BOLIVIA: Pando	11	17.2 ± 0.28	16.6–17.5
BOLIVIA: La Paz	48	17.0 ± 0.71	15.0–18.2
BOLIVIA: Beni	17	16.5 ± 0.66	15.1–17.6
BOLIVIA: Santa Cruz-1	26	16.4 ± 0.63	15.1–17.6
BOLIVIA: Santa Cruz-2	21	16.7 ± 0.71	15.0–18.0
BOLIVIA: Santa Cruz-3	21	16.6 ± 0.59	15.7–18.1
BOLIVIA: Santa Cruz-4	26	16.6 ± 0.54	15.7–18.0
O. emmonsae			
BRAZIL: Pará	14	16.6 ± 0.67	15.7–18.0
O. russatus			
BOLIVIA: Chuquisaca	15	17.9 ± 0.66	17.0–19.4
BOLIVIA: Tarija	11	17.8 ± 0.68	16.4–18.5
ARGENTINA: Salta + Jujuy	14	17.6 ± 0.29	17.1–18.1
BRAZIL: São Paulo	38	18.1 ± 0.57	17.1–19.5
BRAZIL: ES + MG	12	18.1 ± 0.64	16.7–19.1
BRAZIL: MG + Goiás	13	18.7 ± 0.55	17.5–19.6
Interorbital breadth			
O. macconnelli			
GUIANAS	17	5.4 ± 0.17	5.2–5.7
VENEZUELA: Bolívar	19	5.4 ± 0.19	5.1–5.8
ECUADOR + PERÚ	32	5.4 ± 0.26	5.0–6.1
PERÚ: Cuzco	10	5.4 ± 0.14	5.2–5.6
BRAZIL: Amazonas	12	5.5 ± 0.22	5.1–5.8
BRAZIL: W Pará	20	5.2 ± 0.26	4.5–5.6
BRAZIL: E Pará	20	5.1 ± 0.15	4.9–5.4
BRAZIL: Amapá	21	5.4 ± 0.20	5.1–5.8
O. nitidus			
PERÚ: Ucayali + Junín	22	5.1 ± 0.22	4.6–5.4
PERÚ: Madre de Dios	42	5.1 ± 0.20	4.7–5.5
BOLIVIA: Pando	11	5.2 ± 0.17	4.9–5.5
BOLIVIA: La Paz	48	5.2 ± 0.21	4.7–5.7
BOLIVIA: Beni	17	5.1 ± 0.20	4.8–5.5
BOLIVIA: Santa Cruz-1	26	5.1 ± 0.17	4.8–5.5
BOLIVIA: Santa Cruz-2	21	5.2 ± 0.20	4.8–5.8
BOLIVIA: Santa Cruz-3	21	5.2 ± 0.22	4.8–5.6
BOLIVIA: Santa Cruz-4	26	5.2 ± 0.18	4.8–5.6
O. emmonsae			
BRAZIL: Pará	14	5.0 ± 0.25	4.6–5.4

Sample	*N*	Mean ± SD	Observed range
O. russatus			
BOLIVIA: Chuquisaca	15	5.6 ± 0.19	5.3–5.9
BOLIVIA: Tarija	11	5.7 ± 0.17	5.3–5.9
ARGENTINA: Salta + Jujuy	14	5.8 ± 0.17	5.6–6.0
BRAZIL: São Paulo	38	5.5 ± 0.23	5.0–6.2
BRAZIL: ES + MG	12	5.4 ± 0.24	5.0–5.8
BRAZIL: MG + Goiás	13	5.8 ± 0.27	5.4–6.4
Length of rostrum			
O. macconnelli			
GUIANAS	17	10.8 ± 0.63	10.8–11.9
VENEZUELA: Bolívar	19	11.5 ± 0.49	10.5–12.5
ECUADOR + PERÚ	32	10.9 ± 0.59	10.9–12.2
PERÚ: Cuzco	10	11.1 ± 0.68	11.1–12.2
BRAZIL: Amazonas	12	11.0 ± 0.38	10.5–11.7
BRAZIL: W Pará	20	10.9 ± 0.58	10.0–11.8
BRAZIL: E Pará	20	10.9 ± 0.50	9.8–12.0
BRAZIL: Amapá	21	10.8 ± 0.70	10.0–12.9
O. nitidus			
PERÚ: Ucayali + Junín	22	11.0 ± 0.61	9.6–12.0
PERÚ: Madre de Dios	42	10.9 ± 0.45	9.8–11.7
BOLIVIA: Pando	11	10.9 ± 0.44	10.2–11.5
BOLIVIA: La Paz	48	11.1 ± 0.65	9.9–12.5
BOLIVIA: Beni	17	11.0 ± 0.49	10.4–11.7
BOLIVIA: Santa Cruz-1	26	10.7 ± 0.57	9.8–12.0
BOLIVIA: Santa Cruz-2	21	11.2 ± 0.68	9.9–12.5
BOLIVIA: Santa Cruz-3	21	10.9 ± 0.47	10.0–11.8
BOLIVIA: Santa Cruz-4	26	10.7 ± 0.52	9.8–11.6
O. emmonsa			
BRAZIL: Pará	14	10.9 ± 0.62	10.2–12.2
O. russatus			
BOLIVIA: Chuquisaca	15	12.0 ± 0.66	10.9–13.5
BOLIVIA: Tarija	11	11.9 ± 0.68	10.4–12.9
ARGENTINA: Salta + Jujuy	14	11.7 ± 0.35	11.1–12.2
BRAZIL: São Paulo	38	11.6 ± 0.55	10.7–11.6
BRAZIL: ES + MG	12	11.6 ± 0.52	10.6–12.3
BRAZIL: MG + Goiás	13	12.6 ± 0.55	11.7–13.4
Breadth of rostrum			
O. macconnelli			
GUIANAS	17	6.4 ± 0.36	5.7–6.9
VENEZUELA: Bolívar	19	6.7 ± 0.32	5.9–7.2
ECUADOR + PERÚ	32	6.4 ± 0.39	5.4–7.2
PERÚ: Cuzco	10	6.4 ± 0.35	5.8–6.8
BRAZIL: Amazonas	12	6.5 ± 0.34	6.0–7.0
BRAZIL: W Pará	20	6.3 ± 0.39	5.4–6.8
BRAZIL: E Pará	20	6.3 ± 0.35	5.5–7.0
BRAZIL: Amapá	21	6.5 ± 0.47	5.5–7.3

Sample	*N*	Mean ± SD	Observed range
O. nitidus			
PERÚ: Ucayali + Junín	22	6.6 ± 0.48	5.5–7.0
PERÚ: Madre de Dios	42	6.2 ± 0.37	5.3–6.9
BOLIVIA: Pando	11	6.4 ± 0.32	6.0–6.9
BOLIVIA: La Paz	48	6.3 ± 0.35	5.6–7.2
BOLIVIA: Beni	17	6.2 ± 0.32	5.4–6.7
BOLIVIA: Santa Cruz-1	26	6.2 ± 0.36	5.4–7.0
BOLIVIA: Santa Cruz-2	21	6.4 ± 0.28	5.9–6.9
BOLIVIA: Santa Cruz-3	21	6.3 ± 0.28	5.8–6.8
BOLIVIA: Santa Cruz-4	26	6.2 ± 0.34	5.8–7.1
O. emmonsae			
BRAZIL: Pará	14	6.3 ± 0.53	5.5–7.4
O. russatus			
BOLIVIA: Chuquisaca	15	6.7 ± 0.40	6.1–7.5
BOLIVIA: Tarija	11	6.6 ± 0.25	6.0–6.9
ARGENTINA: Salta + Jujuy	14	6.7 ± 0.36	6.3–7.8
BRAZIL: São Paulo	38	6.7 ± 0.42	5.6–7.6
BRAZIL: ES + MG	12	6.8 ± 0.50	6.0–7.5
BRAZIL: MG + Goiás	13	7.3 ± 0.35	6.9–8.2
Lambdoidal breadth			
O. macconnelli			
GUIANAS	17	12.3 ± 0.47	11.5–13.3
VENEZUELA: Bolívar	19	12.5 ± 0.43	11.8–13.5
ECUADOR + PERÚ	32	12.4 ± 0.36	11.9–13.2
PERÚ: Cuzco	10	12.4 ± 0.29	11.9–12.9
BRAZIL: Amazonas	12	12.8 ± 0.38	12.2–13.5
BRAZIL: W Pará	20	12.0 ± 0.45	11.3–12.8
BRAZIL: E Pará	20	12.3 ± 0.28	11.7–12.8
BRAZIL: Amapá	21	12.1 ± 0.33	11.2–12.5
O. nitidus			
PERÚ: Ucayali + Junín	22	12.5 ± 0.39	11.9–13.2
PERÚ: Madre de Dios	42	12.3 ± 0.53	11.3–13.4
BOLIVIA: Pando	11	12.4 ± 0.38	11.6–12.9
BOLIVIA: La Paz	48	12.5 ± 0.37	11.7–13.3
BOLIVIA: Beni	17	12.3 ± 0.40	11.7–12.3
BOLIVIA: Santa Cruz-1	26	12.2 ± 0.48	11.4–13.3
BOLIVIA: Santa Cruz-2	21	12.5 ± 0.43	11.8–13.4
BOLIVIA: Santa Cruz-3	21	12.2 ± 0.42	11.1–12.2
BOLIVIA: Santa Cruz-4	26	12.2 ± 0.34	11.6–12.9
O. emmonsae			
BRAZIL: Pará	14	11.7 ± 0.54	11.0–12.7
O. russatus			
BOLIVIA: Chuquisaca	15	12.7 ± 0.46	11.8–13.2
BOLIVIA: Tarija	11	12.9 ± 0.29	12.1–13.1
ARGENTINA: Salta + Jujuy	14	12.7 ± 0.22	12.4–13.1
BRAZIL: São Paulo	38	12.8 ± 0.40	11.9–13.5

Sample	*N*	Mean ± SD	Observed range
O. russatus			
BRAZIL: ES + MG	12	12.9 ± 0.52	12.2–13.7
BRAZIL: MG + Goiás	13	13.2 ± 0.35	12.6–13.8
Height of braincase			
O. macconnelli			
GUIANAS	17	8.8 ± 0.38	8.1–9.6
VENEZUELA: Bolívar	19	9.0 ± 0.30	8.5–9.5
ECUADOR + PERÚ	32	8.9 ± 0.34	8.3–9.7
PERÚ: Cuzco	10	9.2 ± 0.18	8.9–9.5
BRAZIL: Amazonas	12	9.2 ± 0.39	8.5–10.1
BRAZIL: W Pará	20	8.7 ± 0.35	8.1–9.4
BRAZIL: E Pará	20	8.8 ± 0.34	8.2–9.5
BRAZIL: Amapá	21	8.8 ± 0.31	8.1–9.4
O. nitidus			
PERÚ: Ucayali + Junín	22	9.0 ± 0.30	8.4–9.5
PERÚ: Madre de Dios	42	8.9 ± 0.38	8.3–10.0
BOLIVIA: Pando	11	9.1 ± 0.23	8.7–9.5
BOLIVIA: La Paz	48	9.0 ± 0.36	8.1–9.9
BOLIVIA: Beni	17	8.7 ± 0.28	8.2–9.0
BOLIVIA: Santa Cruz-1	26	8.9 ± 0.32	8.3–9.4
BOLIVIA: Santa Cruz-2	21	9.1 ± 0.44	8.2–9.9
BOLIVIA: Santa Cruz-3	21	8.9 ± 0.39	8.2–9.8
BOLIVIA: Santa Cruz-4	26	8.9 ± 0.29	8.4–9.5
O. emmonsae			
BRAZIL: Pará	14	8.9 ± 0.37	8.2–9.5
O. russatus			
BOLIVIA: Chuquisaca	15	9.1 ± 0.36	8.5–9.9
BOLIVIA: Tarija	11	9.0 ± 0.25	8.7–9.4
ARGENTINA: Salta + Jujuy	14	9.1 ± 0.25	8.6–9.6
BRAZIL: São Paulo	38	9.3 ± 0.32	8.6–10.0
BRAZIL: ES + MG	12	9.5 ± 0.33	9.0–10.0
BRAZIL: MG + Goiás	13	9.6 ± 0.35	9.2–10.5
Breadth of zygomatic plate			
O. macconnelli			
GUIANAS	17	3.4 ± 0.20	3.1–3.9
VENEZUELA: Bolívar	19	3.6 ± 0.20	3.2–4.0
ECUADOR + PERÚ	32	3.6 ± 0.27	3.0–4.1
PERÚ: Cuzco	10	3.5 ± 0.25	3.1–3.8
BRAZIL: Amazonas	12	3.5 ± 0.14	3.3–3.8
BRAZIL: W Pará	20	3.2 ± 0.18	3.0–3.6
BRAZIL: E Pará	20	3.3 ± 0.16	3.0–3.6
BRAZIL: Amapá	21	3.4 ± 0.23	3.0–3.9
O. nitidus			
PERÚ: Ucayali + Junín	22	4.0 ± 0.33	3.4–4.4
PERÚ: Madre de Dios	42	3.9 ± 0.27	3.3–4.5
BOLIVIA: Pando	11	3.9 ± 0.27	3.5–4.5
BOLIVIA: La Paz	48	4.0 ± 0.31	3.4–4.8
BOLIVIA: Beni	17	3.9 ± 0.26	3.6–4.5
BOLIVIA: Santa Cruz-1	26	3.9 ± 0.29	3.4–4.6
BOLIVIA: Santa Cruz-2	21	4.1 ± 0.27	3.5–4.4
BOLIVIA: Santa Cruz-3	21	3.8 ± 0.16	3.5–4.0
BOLIVIA: Santa Cruz-4	26	3.9 ± 0.20	3.6–4.4
O. emmonsae			
BRAZIL: Pará	14	3.5 ± 0.26	3.1–4.0
O. russatus			
BOLIVIA: Chuquisaca	15	4.3 ± 0.26	3.7–4.8
BOLIVIA: Tarija	11	4.3 ± 0.39	3.4–4.7
ARGENTINA: Salta + Jujuy	14	4.2 ± 0.18	3.9–4.5
BRAZIL: São Paulo	38	4.2 ± 0.29	3.7–4.8
BRAZIL: ES + MG	12	3.9 ± 0.27	3.5–4.3
BRAZIL: MG + Goiás	13	4.6 ± 0.26	4.2–5.2
Length of diastema			
O. macconnelli			
GUIANAS	17	8.6 ± 0.52	7.6–9.5
VENEZUELA: Bolívar	19	8.8 ± 0.38	8.3–9.5
ECUADOR + PERÚ	32	8.6 ± 0.42	7.7–9.7
PERÚ: Cuzco	10	8.6 ± 0.32	8.3–9.3
BRAZIL: Amazonas	12	9.0 ± 0.33	8.5–9.5
BRAZIL: W Pará	20	8.3 ± 0.54	7.4–9.2
BRAZIL: E Pará	20	8.6 ± 0.41	7.9–9.3
BRAZIL: Amapá	21	8.5 ± 0.40	8.0–9.6
O. nitidus			
PERÚ: Ucayali + Junín	22	8.4 ± 0.47	7.4–9.1
PERÚ: Madre de Dios	42	8.3 ± 0.49	7.4–9.3
BOLIVIA: Pando	11	8.5 ± 0.49	7.8–9.5
BOLIVIA: La Paz	48	8.7 ± 0.45	7.8–9.5
BOLIVIA: Beni	17	8.5 ± 0.39	8.0–9.2
BOLIVIA: Santa Cruz-1	26	8.5 ± 0.47	7.6–9.5
BOLIVIA: Santa Cruz-2	21	8.6 ± 0.53	7.8–9.5
BOLIVIA: Santa Cruz-3	21	8.7 ± 0.35	7.9–9.2
BOLIVIA: Santa Cruz-4	26	8.4 ± 0.43	7.7–9.7
O. emmonsae			
BRAZIL: Pará	14	8.2 ± 0.60	7.4–9.1
O. russatus			
BOLIVIA: Chuquisaca	15	8.7 ± 0.48	7.9–9.7
BOLIVIA: Tarija	11	8.5 ± 0.44	7.7–9.3
ARGENTINA: Salta + Jujuy	14	8.4 ± 0.22	8.2–8.8
BRAZIL: São Paulo	38	8.5 ± 0.43	7.6–9.4
BRAZIL: ES + MG	12	8.8 ± 0.29	8.3–9.3
BRAZIL: MG + Goiás	13	9.6 ± 0.55	8.1–10.5

Sample	*N*	Mean ± SD	Observed range
Length of bony palate			
O. macconnelli			
GUIANAS	17	7.3 ± 0.40	6.8–8.1
VENEZUELA: Bolívar	19	7.6 ± 0.35	6.9–8.3
ECUADOR + PERÚ	32	7.0 ± 0.43	6.3–8.2
PERÚ: Cuzco	10	7.1 ± 0.34	6.5–7.8
BRAZIL: Amazonas	12	7.7 ± 0.27	7.2–8.2
BRAZIL: W Pará	20	6.9 ± 0.44	6.3–7.8
BRAZIL: E Pará	20	7.4 ± 0.35	6.8–8.3
BRAZIL: Amapá	21	7.5 ± 0.45	6.9–8.4
O. nitidus			
PERÚ: Ucayali+ Junín	22	6.7 ± 0.42	5.9–7.6
PERÚ: Madre de Dios	42	6.6 ± 0.39	5.7–7.6
BOLIVIA: Pando	11	6.5 ± 0.36	6.0–7.2
BOLIVIA: La Paz	48	6.7 ± 0.34	5.8–7.4
BOLIVIA: Beni	17	6.6 ± 0.26	6.1–7.2
BOLIVIA: Santa Cruz-1	26	6.2 ± 0.33	5.7–6.9
BOLIVIA: Santa Cruz-2	21	6.3 ± 0.41	5.6–7.1
BOLIVIA: Santa Cruz-3	21	6.4 ± 0.29	5.9–7.0
BOLIVIA: Santa Cruz-4	26	6.3 ± 0.23	5.9–6.7
O. emmonsae			
BRAZIL: Pará	14	6.8 ± 0.30	6.2–7.3
O. russatus			
BOLIVIA: Chuquisaca	15	7.1 ± 0.28	6.4–7.5
BOLIVIA: Tarija	11	7.0 ± 0.19	6.6–7.2
ARGENTINA: Salta + Jujuy	14	7.1 ± 0.25	6.6–7.5
BRAZIL: São Paulo	38	6.6 ± 0.37	5.8–7.4
BRAZIL: ES + MG	12	6.5 ± 0.20	6.1–6.7
BRAZIL: MG + Goiás	13	7.6 ± 0.35	7.2–8.3
Postpalatal length			
O. macconnelli			
GUIANA	17	10.9 ± 0.48	10.0–11.9
VENEZUELA: Bolívar	19	11.6 ± 0.53	10.2–12.5
ECUADOR + PERÚ	32	11.4 ± 0.60	9.7–12.3
PERÚ: Cuzco	10	11.0 ± 0.51	10.4–12.0
BRAZIL: Amazonas	12	11.6 ± 0.33	11.1–12.2
BRAZIL: W Pará	20	10.9 ± 0.54	9.9–11.9
BRAZIL: E Pará	20	10.8 ± 0.43	9.9–11.6
BRAZIL: Amapá	21	10.6 ± 0.60	9.5–11.9
O. nitidus			
PERÚ: Ucayali + Junín	22	11.3 ± 0.57	10.1–12.2
PERÚ: Madre de Dios	42	11.2 ± 0.49	10.3–12.6
BOLIVIA: Pando	11	11.3 ± 0.42	10.4–11.7
BOLIVIA: La Paz	48	11.4 ± 0.59	10.2–12.6
BOLIVIA: Beni	17	11.2 ± 0.46	10.4–12.1
BOLIVIA: Santa Cruz-1	26	11.1 ± 0.56	9.9–12.3
BOLIVIA: Santa Cruz-2	21	11.6 ± 0.37	10.6–12.1
BOLIVIA: Santa Cruz-3	21	11.4 ± 0.46	10.5–12.1
BOLIVIA: Santa Cruz-4	26	11.3 ± 0.56	10.2–12.9
O. emmonsae			
BRAZIL: Pará	14	11.3 ± 0.68	10.0–12.6
O. russatus			
BOLIVIA: Chuquisaca	15	12.0 ± 0.55	11.0–13.0
BOLIVIA: Tarija	11	11.9 ± 0.53	10.7–12.6
ARGENTINA: Salta + Jujuy	14	11.8 ± 0.30	11.2–12.4
BRAZIL: São Paulo	38	12.3 ± 0.51	11.3–13.4
BRAZIL: ES + MG	12	12.4 ± 0.48	11.6–12.9
BRAZIL: MG + Goiás	13	12.0 ± 0.52	10.7–12.5
Length of incisive foramina			
O. macconnelli			
GUIANAS	17	5.1 ± 0.35	4.5–6.0
VENEZUELA: Bolívar	19	5.3 ± 0.23	4.9–5.7
ECUADOR + PERÚ	32	5.3 ± 0.30	4.9–6.0
PERÚ: Cuzco	10	5.1 ± 0.32	4.7–5.6
BRAZIL: Amazonas	12	5.2 ± 0.32	4.5–5.8
BRAZIL: W Pará	20	5.1 ± 0.31	4.4–5.8
BRAZIL: E Pará	20	5.2 ± 0.25	4.7–5.5
BRAZIL: Amapá	21	5.1 ± 0.29	4.4–5.6
O. nitidus			
PERÚ: Ucayali + Junín	22	5.6 ± 0.41	4.6–6.2
PERÚ: Madre de Dios	42	5.5 ± 0.32	4.8–6.3
BOLIVIA: Pando	11	5.7 ± 0.28	5.2–6.1
BOLIVIA: La Paz	48	5.8 ± 0.35	5.0–6.8
BOLIVIA: Beni	17	5.5 ± 0.22	5.0–5.8
BOLIVIA: Santa Cruz-1	26	5.5 ± 0.33	4.8–6.0
BOLIVIA: Santa Cruz-2	21	5.6 ± 0.28	5.1–6.1
BOLIVIA: Santa Cruz-3	21	5.6 ± 0.21	5.1–5.9
BOLIVIA: Santa Cruz-4	26	5.6 ± 0.37	4.8–6.5
O. emmonsae			
BRAZIL: Pará	14	5.0 ± 0.31	4.5–5.6
O. russatus			
BOLIVIA: Chuquisaca	15	5.6 ± 0.34	5.1–6.3
BOLIVIA: Tarija	11	5.3 ± 0.25	4.9–5.6
ARGENTINA: Salta + Jujuy	14	5.1 ± 0.23	4.8–5.6
BRAZIL: São Paulo	38	5.7 ± 0.29	5.0–6.5
BRAZIL: ES + MG	12	6.0 ± 0.20	5.6–6.3
BRAZIL: MG + Goiás	13	6.1 ± 0.51	4.9–6.8
Breadth of incisive foramina			
O. macconnelli			
GUIANAS	17	2.7 ± 0.20	2.3–3.0
VENEZUELA: Bolívar	19	2.9 ± 0.14	2.6–3.2
ECUADOR + PERÚ	32	2.7 ± 0.22	2.3–3.1
PERÚ: Cuzco	10	2.4 ± 0.20	2.0–2.6
BRAZIL: Amazonas	12	2.7 ± 0.25	2.2–3.1
BRAZIL: W Pará	20	2.6 ± 0.19	2.2–3.0

Sample	*N*	Mean ± SD	Observed range
O. macconnelli			
BRAZIL: E Pará	20	2.5 ± 0.16	2.1–2.8
BRAZIL: Amapá	21	2.6 ± 0.17	2.3–3.1
O. nitidus			
PERÚ: Ucayali + Junín	22	2.2 ± 0.11	2.0–2.4
PERÚ: Madre de Dios	42	2.1 ± 0.15	1.8–2.5
BOLIVIA: Pando	11	2.1 ± 0.18	1.9–2.4
BOLIVIA: La Paz	48	2.3 ± 0.14	2.0–2.6
BOLIVIA: Beni	17	2.2 ± 0.16	1.9–2.4
BOLIVIA: Santa Cruz-1	26	2.1 ± 0.15	1.8–2.5
BOLIVIA: Santa Cruz-2	21	2.3 ± 0.16	2.0–2.5
BOLIVIA: Santa Cruz-3	21	2.3 ± 0.16	2.1–2.6
BOLIVIA: Santa Cruz-4	26	2.2 ± 0.13	2.0–2.6
O. emmonsae			
BRAZIL: Pará	14	2.4 ± 0.18	2.1–2.8
O. russatus			
BOLIVIA: Chuquisaca	15	2.2 ± 0.18	1.9–2.5
BOLIVIA: Tarija	11	2.2 ± 0.09	2.1–2.4
ARGENTINA: Salta + Jujuy	14	2.2 ± 0.09	2.0–3.0
BRAZIL: São Paulo	38	2.2 ± 0.14	2.0–2.5
BRAZIL: ES + MG	12	2.5 ± 0.17	2.2–2.9
BRAZIL: MG + Goiás	13	2.1 ± 0.17	1.7–2.4
Crown length of M1–3			
O. macconnelli			
GUIANAS	17	4.9 ± 0.13	4.6–5.1
VENEZUELA: Bolívar	19	5.1 ± 0.13	4.8–5.3
ECUADOR + PERÚ	32	5.2 ± 0.20	4.6–5.6
PERÚ: Cuzco	10	5.1 ± 0.23	4.9–5.6
BRAZIL: Amazonas	12	5.1 ± 0.11	5.0–5.3
BRAZIL: W Pará	20	5.0 ± 0.15	4.8–5.3
BRAZIL: E Pará	20	5.1 ± 0.14	4.8–5.4
BRAZIL: Amapá	21	5.0 ± 0.19	4.6–5.2
O. nitidus			
PERÚ: Ucayali + Junín	22	5.0 ± 0.12	4.8–5.2
PERÚ: Madre de Dios	42	5.0 ± 0.16	4.4–5.2
BOLIVIA: Pando	11	4.8 ± 0.13	4.7–5.0
BOLIVIA: La Paz	48	4.9 ± 0.15	4.6–5.1
BOLIVIA: Beni	17	4.8 ± 0.16	4.5–5.1
BOLIVIA: Santa Cruz-1	26	4.7 ± 0.11	4.5–4.9
BOLIVIA: Santa Cruz-2	21	4.8 ± 0.15	4.5–5.1
BOLIVIA: Santa Cruz-3	21	4.8 ± 0.11	4.6–5.0
BOLIVIA: Santa Cruz-4	26	4.8 ± 0.14	4.5–5.2
O. emmonsae			
BRAZIL: Pará	14	4.9 ± 0.15	4.7–5.1
O. russatus			
BOLIVIA: Chuquisaca	15	5.1 ± 0.13	4.9–5.4
BOLIVIA: Tarija	11	5.2 ± 0.13	5.0–5.4
ARGENTINA: Salta + Jujuy	14	5.1 ± 0.11	4.9–5.3
BRAZIL: São Paulo	38	5.2 ± 0.14	4.9–5.5
BRAZIL: ES + MG	12	5.1 ± 0.12	5.0–5.4
BRAZIL: MG + Goiás	13	5.1 ± 0.11	5.0–5.3
Breadth of M1			
O. macconnelli			
GUIANAS	17	1.4 ± 0.08	1.3–1.6
VENEZUELA: Bolívar	19	1.5 ± 0.07	1.4–1.6
ECUADOR + PERÚ	32	1.5 ± 0.10	1.4–1.7
PERÚ: Cuzco	10	1.5 ± 0.10	1.3–1.6
BRAZIL: Amazonas	12	1.6 ± 0.05	1.5–1.6
BRAZIL: W Pará	20	1.4 ± 0.06	1.3–1.5
BRAZIL: E Pará	20	1.5 ± 0.07	1.4–1.7
BRAZIL: Amapá	21	1.5 ± 0.05	1.4–1.6
O. nitidus			
PERÚ: Ucayali + Junín	22	1.4 ± 0.06	1.3–1.5
PERÚ: Madre de Dios	42	1.5 ± 0.06	1.3–1.6
BOLIVIA: Pando	12	1.5 ± 0.05	1.4–1.5
BOLIVIA: La Paz	48	1.5 ± 0.06	1.4–1.6
BOLIVIA: Beni	17	1.5 ± 0.05	1.4–1.5
BOLIVIA: Santa Cruz-1	26	1.4 ± 0.06	1.3–1.5
BOLIVIA: Santa Cruz-2	21	1.5 ± 0.06	1.3–1.5
BOLIVIA: Santa Cruz-3	21	1.5 ± 0.06	1.3–1.5
BOLIVIA: Santa Cruz-4	26	1.5 ± 0.07	1.3–1.6
O. emmonsae			
BRAZIL: Pará	14	1.4 ± 0.05	1.4–1.5
O. russatus			
BOLIVIA: Chuquisaca	15	1.6 ± 0.06	1.5–1.7
BOLIVIA: Tarija	11	1.6 ± 0.07	1.4–1.6
ARGENTINA: Salta + Jujuy	14	1.6 ± 0.05	1.5–1.6
BRAZIL: São Paulo	38	1.5 ± 0.06	1.4–1.7
BRAZIL: ES + MG	12	1.6 ± 0.09	1.5–1.8
BRAZIL: MG + Goiás	13	1.6 ± 0.06	1.5–1.7

APPENDIX F

List of Measured Specimens of the *Oryzomys nitidus* Group

Below we list the adults measured of *Oryzomys macconnelli*, *O. nitidus*, *O. emmonsae,* and *O. russatus*. The specimens form the population samples from which the descriptive statistics listed in appendix E and the multivariate statistical analyses were derived. Each sample is identified by number and name that correspond to the numbered samples described in table 39.

Oryzomys macconnelli

1. **GUIANAS: French Guiana + Surinam + Guyana**
   BMNH 10.5.4.29, 10.5.4.30, 10.5.4.32, 10.5.4.34 (holotype of *O. macconnelli*), 12.6.5.23; CM 54058, 54059, 64561; MNHN 1983-367, 1983-371–1983-373, 1986-276, 1994-126, 1994-127, 1995-208; USNM 578018
2. **VENEZUELA: Bolívar**
   AMNH 130880, 130908, 130913, 130928, 130961, 130965, 130970, 130974, 130975, 130983, 131119, 131128, 257238; MHNLS 7831, 7836, 8075, 8076; USNM 448584, 448585
3. **ECUADOR: Pastaza + PERÚ: Loreto**
   AMNH 71553, 71577–71583, 71585–71588; BMNH 54.442, 54.444, 54.446–54.448, 54.450–54.454, 54.458, 54.459, 54.471; NW 858, 870, 871, 881, 897; RMT 4080, 4087
4. **PERÚ: Cuzco**
   FMNH 66395, 66397, 68633, 75271, 75274, 75275, 75278, 75279, 75286; USNM 194564
5. **BRAZIL: Amazonas**
   JLP 15548, 15549, 15563, 15600, 15619, 15859; MNFS 529, 530, 549, 550, 563, 747
6. **BRAZIL: W Pará**
   USNM 461784, 461785, 521533–521535, 544606–544608, 544610–544612, 544615, 544616, 544619–544623, 545293, 545294
7. **BRAZIL: E Pará**
   AMNH 188967, 188968, 203403–203415; USNM 519772–519774, 519776, 521437
8. **BRAZIL: Amapá**
   USNM 394207–394209, 394211, 394212, 394214–394221, 394224–394227, 394229, 394230, 394232, 543355

Oryzomys nitidus

9. **PERÚ: central: Ucayali + Junín**
   BMNH 85.4.1.0, 85.4.1.10a, 85.4.1.10b; LSUMZ 12333–12336, 12338–12343, 14356, 14357, 14365, 16690; MVZ 136573, 136574, 136576, 136578, 136588
10. **PERÚ: Madre de Dios**
    KU 144458–144462, 144464–144468, 144470, 144471, 144474, 144475, 144477, 144480, 144481, 144484, 144487–144493, 144497, 144499, 144500, 144502–144505, 144507, 144508, 144510, 144511, 144513–144517; USNM 390068
11. **BOLIVIA: Pando**
    AMNH 248991, 262948, 262960–262962, 262964, 262965, 262967; MSB 57116, 57117, 57119
12. **BOLIVIA: La Paz**
    AMNH 264733, 264734, 264736, 264738–264745, 264747, 264748, 264751–264755, 264757–264765, 265767; MSB 68450–68452, 68454, 68456–68470, 68472
13. **BOLIVIA: Beni**
    AMNH 211746, 255955, 262052, 262054, 262056, 262057, 262094, 262096, 263494; MSB 56056, 56057, 68448, 68449; USNM 390054–390056, 390058
14. **BOLIVIA: Santa Cruz-1**
    AMNH 211716, 211732, 211733, 211735–211738, 211741, 260353, 260354, 260356, 260357, 260359, 260360, 260363, 260364, 262045, 262046; MSB 51062, 55328–55334
15. **BOLIVIA: Santa Cruz-2**
    AMNH 262026, 262035, 262036, 262038–262040, 262042, 262075, 262083, 262087–262089, 262365; MSB 56063, 56066–56068, 56070, 56360, 56362, 56364
16. **BOLIVIA: Santa Cruz-3**
    USNM 390072, 390073, 390076–390083, 390085, 390090–390092, 390094, 390098, 390100–390102, 390104, 390105
17. **BOLIVIA: Santa Cruz-4**
    AMNH 260366–260372, 263873, 263874, 263876–263879, 264183; MSB 55335, 55337, 59878-59882, 67322, 67323, 63356–63358

Oryzomys emmonsae

18. **BRAZIL: Pará**
    MZUSP 27150 (holotype of *O. emmonsae*); USNM 521530, 543327–543329, 543331, 543332, 543334–543338, 549551, 549552

Oryzomys russatus

19. **BOLIVIA: Chuquisaca**
    AMNH 263881, 263882–263887; MSB 63359, 63360, 63584; USNM 270914, 271583–271585, 271587
20. **BOLIVIA: Tarija**
    AMNH 264190, 264186–264189; BMNH 25.2.1.24 (holotype of *O. legatus*); MSB 67319, 67320, 67358, 67359; UMMZ 155888
21. **ARGENTINA: Salta + Jujuy**

ARG 3414, 3446, 3449, 3450, 3471; CM 43819–43826, 72391

22. BRAZIL: São Paulo
USNM 461985, 461989, 484022, 484026–484038, 484040–484042, 485001, 485002, 485004–485007, 485011–485018, 485020, 485021, 542922, 542927, 542928

23. BRAZIL: Espírito Santo + Minas Gerais
AMNH 203073 (holotype of *O. kelloggi*); LACM 62898, 62900–62902; USNM 304562–304565, 304567, 304569, 332452

24. BRAZIL: Minas Gerais + Goiás
AMNH 134644, 134663–134667, 134677, 134763, 134772: BMNH 1.11.3.30, 1.11.3.32 (holotype of *O. lamia*), 1.11.3.33, 1.11.3.34

APPENDIX G

Records of *Oryzomys megacephalus*, *Oryzomys nitidus*, and *Oryzomys macconnelli* Collected with *Oryzomys yunganus*

Below we record the specimens of *O. megacephalus*, *O. nitidus*, and *O. macconnelli* that were collected with examples of *O. yunganus* at localities in French Guiana, Surinam, Guyana, Venezuela, Colombia, Ecuador, Perú, Bolivia, and Brazil. The number in parentheses at the left of each locality refers to the corresponding numbered locality in the gazetteer for *O. yunganus* and to the numbered symbol on the map in figure 14; specimens of *O. yunganus* from each place are listed in the gazetteer. Next to each locality we indicate the period of time (placed in parentheses) during which samples of the sympatric species combinations were collected.

FRENCH GUIANA

(1) ARATAYE (1986)
O. megacephalus MNHN 1986-288–1986-291, 1986-293, 1986-295, 1986-296, 1986-300, 1986-301

(3) ÎLE DE CAYENNE (1986)
O. megacephalus MNHN 1986-319

(4) CACAO (1986)
O. megacephalus MNHN 1986-316, 1986-488, 1986-493, 1986-495–1986-501, 1986-505, 1986-509, 1986-511

(5) PARACOU (June–Aug 1991; Oct, Nov 1992; Aug 1993)
O. megacephalus AMNH 266494, 266497–266499, 266501, 266502, 266504, 266505, 266507–266509, 266514, 266515, 266518, 266519, 266521, 266523, 266525, 266527–266530, 266533–266541, 267015, 267016, 267018, 267566

SURINAM

(10) TAFELBERG (Oct, Nov 1981)
O. megacephalus CM 76932, 76934, 76935

(11) KAISER GEBERGTE (Nov 1960; Jan 1961)
O. megacephalus FMNH 93283, 93285, 93287–93289

GUYANA

(12) KWABANNA (Mar 1991)
O. megacephalus ROM 98723, 98737, 98739, 98751, 98752

(13) SANTA CRUZ (Apr 1991)
O. megacephalus ROM 98795, 98827, 98838

VENEZUELA

(14) AUYÁN TEPUY (Dec 1937; Jan–Mar 1938)
O. megacephalus AMNH 130876, 130878, 130879, 130881, 130893–130895, 130897, 130900, 130904, 130909, 130910, 130912, 130917–130919, 130922, 130925, 130927, 130929, 130930, 130935, 130936, 130938, 130939, 130942, 130944–130947, 130951, 130953, 130954, 130956, 130957, 130963, 130964, 130966–130969, 131094, 131095, 131097, 131099, 131120, 131122–131124
O. macconnelli AMNH 130877, 130880, 130882, 130907, 130908, 130911, 130913, 130920, 130926, 130928, 130931, 130958, 130961, 130965, 130970, 130971, 131098, 131100, 131102, 131111, 131119, 131121

(15) ARABOPÓ (Dec 1927; Jan 1928)
O. megacephalus AMNH 75756–75769, 75771–75789

(17) TAMATAMA (May 1967)
O. megacephalus USNM 409865, 409867, 409870, 409871, 416708, 442127, 495356–495358, 495362, 495363, 495365

COLOMBIA

(18) GUAICARAMO (1925)
O. megacephalus AMNH 71296–71300, 71312–71327, 71338; USNM 251961, 251964–251966

(18a) VILLAVICENCIO (Mar–May 1939)
O. megacephalus AMNH 136347, 136348, 136352, 136356, 136358, 136360, 136361, 136364, 202644, 202646

(19) RÍO MECAYA (Feb–Mar 1925)
O. megacephalus FMNH 72037–72040, 72043–72047, 72052–72056, 72068–72072, 72091

O. macconnelli FMNH 42041, 72060, 72061

ECUADOR

(23) SAN JOSÉ ABAJO (Mar 1923; Apr 1924)

O. megacephalus AMNH 68047, 68048, 68050, 68060, 68081, 68083–68087, 68099–68101, 68104, 68107, 68116, 68117

O. macconnelli AMNH 64018, 68182, 68183

(29) RÍO CAPAHUARI (Nov 1934)

O. macconnelli FMNH 43266, 43267, 43272–43275

(30) RÍO TIGRE (Mar, Nov 1937)

O. megacephalus BMNH 54.435

O. macconnelli BMNH 54.445–54.449, 54.455–54.459

(31) ZAMORA (Nov–Dec 1920)

O. megacephalus AMNH 47820–47823, 47826–47829, 47557

PERÚ

(32) BOCA DEL RÍO CURARAY (Oct–Dec 1925)

O. megacephalus AMNH 71556, 71558–71569, 71571–71574

O. macconnelli AMNH 71553, 71577–71583, 71585–71588

(33) HUACHI (Jan, May, Sept 1937)

O. megacephalus BMNH 54.423, 54.424

O. macconnelli BMNH 54.442, 54.451–54.454

(39) RIOJA (July 1912)

O. nitidus FMNH 19793

(40) MOYOBAMBA (July 1912)

O. nitidus FMNH 19380, 19389

(41) RÍO PACHITEA (Mar 1923)

O. megacephalus BMNH 23.10.16.22–23.10.16.28, 23.10.16.31–23.10.16.33

(45) POZUZO (Feb 1923)

O. megacephalus FMNH 24566, 126693–126706

(46) SAN PABLO (July 1964)

O. megacephalus AMNH 230968–230979, 231662–231665, 231672, 231673, 231757

(48) PERENÉ (Apr 1921)

O. megacephalus FMNH 18969, 18971, 63869, 63870, 63872, 63874, 63878

(49) BALTA (July, Aug 1966; June, July 1968; Feb, Mar, Apr 1971)

O. megacephalus LSUMZ 12348–12356, 14358–14359, 16680–16684, 16692; MVZ 136575, 136577, 136579, 136580, 136582–136584, 136586, 136589

O. nitidus LSUMZ 12333–12347, 14356, 14357, 14365, 16690, 16691, 16694; MVZ 136573, 136574, 136576, 136578, 136588, 136616

O. macconnelli LSUMZ 14366

(53) QUINCEMIL (June, Aug 1953)

O. megacephalus FMNH 75222, 75241, 75243–75251, 75255, 75256, 75258, 75260, 75265–75267, 75269, 75270, 75273

O. macconnelli FMNH 75268, 75271, 75274–75279

(54) CADENA (May, Aug, Oct, Dec 1949; Feb, Mar 1950)

O. macconnelli FMNH 66395–66397, 68633, 68634

BOLIVIA

(57) BOCA DEL RÍO BIATA (Aug 1986)

O. megacephalus AMNH 262953, 262956, 262959; MSB 57158, 57159, 57167, 57351, 57352

O. nitidus AMNH 262847, 262849, 262850, 262949, 262954, 262955, 262958; MSB 57168

(60) CERRO AMBORÓ (Aug 1985)

O. megacephalus AMNH 262021, 262080

O. macconnelli AMNH 262040, 262042, 262082

BRAZIL

(61) SENA MADUREIRA (June, July 1976)

O. megacephalus USNM 545295, 545297–545299, 545301, 545303, 545305

(62) OPPOSITE PORONGABA (Feb, Mar 1992)

O. megacephalus MNFS 1241–1244, 1246, 1333, 1334, 1340–1346, 1348, 1367, 1369–1372, 1374, 1375, 1388, 1390, 1391, 1405, 1407, 1408

(63) PORONGABA (Feb, Mar 1992)

O. megacephalus MNFS 1100, 1115, 1116, 1120, 1144–1146, 1149, 1168–1170, 1173, 1204–1206, 1227, 1268, 1297, 1329, 1330, 1381, 1400, 1418, 1421–1423

O. nitidus MNFS 1147, 1223, 1309, 1419, 1420

(65) SOBRAL (Mar 1992)

O. megacephalus JUR 216, 218, 219, 246; MNFS 1436, 1454, 1463, 1464, 1466, 1480, 1566

(66) NOVA VIDA (Mar 1992)

O. megacephalus JUR 213, 228, 237; MNFS 1586, 1587, 1597, 1612–1614, 1629, 1651

(67) SERINGAL CONDOR (Sept, Oct 1991)

O. megacephalus JLP 15529, 15536, 15564, 15604, 15609, 15646, 15650, 15687–15689, 15694, 15706, 15707, 15719, 15723, 15726, 15727, 15740

O. macconnelli JLP 15548, 15549, 15563, 15600, 15619; MNFS 529, 530, 548–550, 563

(68) PENEDO (Aug, Sept 1991)

O. megacephalus JLP 15229–15232, 15238–15240, 15242, 15243, 15248, 15249, 15256, 15259, 15272, 15274, 15291, 15311, 15322, 15330–15332, 15362, 15456, 15499, 15507; MNFS 329, 330, 373, 385, 389, 404, 405, 420, 421, 488–490, 498, 510, 518, 520

(69) NOVA EMPRESA (Aug, Sept 1991)

O. megacephalus JLP 15416–15418, 15447; JUR 1, 4, 6, 10–12, 14, 36, 39, 40, 42, 43, 47, 72, 76–79, 114; MNFS 440

(70) OPPOSITE ALTAMIRA (Nov 1991)

O. megacephalus JLP 16030; MNFS 868, 917, 952–954

(71) ALTAMIRA (Nov 1991)

O. megacephalus JLP 15967, 15968, 16026–16029, 16067, 16081; MNFS 897

(72) BARRO VERMELHO (Oct, Nov 1991)

O. megacephalus JLP 15748, 15762, 15763, 15768–15773, 15782, 15783, 15790, 15813, 15829, 15865, 15871, 15872, 15875–15877, 15881–15884, 15892, 15893, 15901; MNFS 682, 685, 686, 736–738, 750, 761, 818, 821, 822, 827, 828

O. macconnelli JLP 15859; MNFS 747

(73) JAINÚ (Oct 1991)

O. megacephalus JLP 15752, 15758, 15822–15825; MNFS 693, 694, 696, 698, 699, 705–707, 712, 713, 716, 751, 765–768, 774–777, 779, 786, 787

(74) COLOCAÇÃO VIRA VOLTA (May, June 1992)

O. megacephalus JUR 418–427, 441–444, 446, 447, 454–456, 465, 473, 481, 482, 490–493, 514–516, 522, 523, 531, 536, 552, 554, 556, 558, 561, 562, 568–570; MNFS 1791

(78) SERRA DO RONCADOR (June–Aug 1968)

O. megacephalus BMNH 81.469, 81.471, 81.475–81.482, 81.484–81.502, 81.504–81.517, 81.524, 81.526–81.530, 81.542, 81.550–81.553, 81.555–81.568, 81.571, 81.582–81.590, 81.592, 86.1130, 86.1131, 86.1135–86.1137, 86.1139–86.1146, 87.638

O. nitidus BMNH 81.436

(79) ALTAMIRA, 54 km S, 150 km W (Nov 1975)

O. megacephalus USNM 521526

O. macconnelli USNM 521438, 521533–521535

(80) ALTAMIRA, 18 km S, 19 km W (Aug, Sept 1975; Apr, May 1976)

O. megacephalus USNM 521443, 521446, 521447, 521450, 521451, 521520, 521522–521525

(81) MACAPÁ (Aug 1967)

O. megacephalus USNM 392061–392064, 392066–392069, 392071–392077

(82) SERRA DO NAVIO

Rio Amapari (June–Dec 1966; Jan–Apr, June, Dec 1967; Feb, Mar, June, Oct 1968)

O. megacephalus USNM 393892, 393894, 393897, 393902, 393911, 393912, 393914, 393917, 393920, 393925, 393926, 393930-393932, 393938–393942, 393953, 393962, 393963, 393967, 393975, 393986, 393990, 393992, 393994, 393995, 394004, 394007, 394008, 394012, 394032, 394033, 394037, 394049, 394051, 394065, 394081, 394083, 394084, 394115, 394132, 394135–394137, 394140, 394141, 394143–394147, 394168, 394174

O. macconnelli USNM 394203, 394204, 394208–394222, 394224–394230, 394232, 543354–543356

Terezinha (Feb 1966)

O. megacephalus USNM 393867, 393870, 393873–393876

Serra C3 (Mar, June, Aug–Oct 1966; Jan–July, Sept–Nov 1967)

O. megacephalus USNM 393879–393883, 393888, 393889, 393898, 393906, 393907, 393922–393924, 393933, 393943–393945, 393947–393949, 393954–393960, 393964, 393966, 393968, 393970–393972, 393974, 393983, 393984, 393997, 394001, 394002, 394010, 394014, 394015, 394018–394020, 394023, 394024, 394026, 394027, 394029–394031, 394035, 394036, 394038, 394047, 394048, 394053–394058, 394060, 394061, 394063, 394064, 394066, 394069, 394072, 394075, 394077–394080, 394082, 394086, 394088–394092, 394094–394096, 394098, 394099, 394102, 394103, 394110–394113, 394116, 394121, 393124–394126, 394133, 394134, 394138, 394142

Estrada de Ferro Amapá, Km 190 (June–Dec 1966; Jan–July, Sept–Nov 1967; Jan–Mar, May–July, Sept–Dec 1968)

O. megacephalus USNM 393884, 393887, 393890, 393891, 393896, 393900, 393903, 393904, 393908, 393909, 393919, 393921, 393927, 393928, 393934–393937, 393950, 393952, 393957, 393973, 393976–393978, 393980–393982, 393985, 393987, 393989, 393991, 393993, 393996, 393998–393400, 394003, 394005, 394009, 394011, 394013, 394016, 394017, 394025, 394028, 394034, 394039, 394040, 394045, 394046, 394062, 394067, 394068, 394070, 394071, 394073, 394085, 394087, 394093, 394100, 394101, 394104, 394107, 394114, 394118, 394120, 394122, 394123, 394127–394131, 394139, 394149, 394150, 394154, 394155, 394157–394161, 394163–394166, 394172, 394173, 394175, 394185, 394187, 394198, 461523, 461524, 461527–461529, 461531, 461533

O. macconnelli USNM 394206, 394207

APPENDIX H

Gazetteers and Specimens of *Hoplomys* and *Sigmodontomys*

We provide here gazetteers of collection localities and specimens examined for the echimyid *Hoplomys gymnurus* and the murid *Sigmodontomys alfari*. Known geographic distributions, as documented by specimens, of these species are generally concordant with the range of *Oryzomys bolivaris* (see figs. 50 and 51, as well as discussion in text). Those localities where examples of *O. bolivaris* were collected with either *Hoplomys* or *Sigmodontomys* are indicated in table 24.

HOPLOMYS GYMNURUS

NICARAGUA

Provincia de Zelaya

1. **Bonanza,** 14°01′N/84°35′W (USBGN Nicaragua, 1976: 9): USNM 338802–338805.

Provincia de Matagalpa

2. **Río Coco** (Allen [1910: 88] placed this locality of Richardson's at 800 ft on the eastern slope of the Caribbean highlands. Buchanan and Howell [1965: 558] estimated the locality to be ‘‘about 10 km. south-east of Quilalí, near the border between the Departments of Nueva Segovia and Jinotega.’’ Jones and Engstrom [1986: 20] did not provide information refuting that location but considered ‘‘it more likely that the village still known in full as San Juan de Río Coco represents Richardson's old collecting locality. San Juan de Río Coco is in the Departamento de Madriz and lies on the old trail between San Juan Telpaneca and Quilalí, both of which were localities at which Richardson obtained mammals. While our location lies only about 15 kilometers west of the one plotted by Buchanan and Howell, it places Río Coco in Madriz rather than in Nuevo Segovia or Jinotega.’’), 13°27′N/85°55′W (determined by Howell, 1986): AMNH 29384, 29385.
3. **Vijagua** (also spelled Bijagua); (Allen [1910: 88] noted that this village was ‘‘on the eastern slope of the highland in Matagalpa Province; altitude probably 1500 to 2000 ft.’’ Buchanan and Howell [1965: 550] wrote that ‘‘Richardson's ‘Vijagua’ is known to be in the Dept. of Matagalpa in the Caribbean slope rain forest. He collected there in mid-March 1909, and at the end of that month he collected specimens that he labeled ‘Rio Tuma.’ On the basis of our tracing of Richardson's movements through his specimens taken at mapped localities before and after March 1909, we think it probable that Vijagua was the name of a small village or hacienda near the Río Tuma, about 35 km north-east of the town of Matagalpa.’’ Jones and Engstrom [1986: 21] agreed with Buchanan and Howell ‘‘as to the approximate location of Vijagua and, in fact, have found two small settlements by that name on old maps that are eight and 10 kilometers south of Peña Blanca (Jinotega), just within the border of Matagalpa and near Guasaca.’’), 13°07N/85°41′W (Jones and Engstrom, 1986: 21): AMNH 29547–29549.
4. **Savala** (‘‘along the inner border of the low east coast region,’’ according to Allen [1910: 87], but Buchanan and Howell [1985: 549] placed Savala more accurately: ‘‘located near the base of the Central Cordillera on the Atlantic drainage; it is approximately 45 km. east-north-east of the city of Matagalpa at an altitude of approximately 260 m.’’), 800 ft: AMNH 28367 (holotype of *Hoplomys truei*), 28368.

COSTA RICA

Provincia de Heredia

5. **Parque Nacional Braulío Carrillo, 11 km S, 4.5 km W Puerto Viejo,** 10°22′N/84°03′W, 280 m (see gazetteer for *Oryzomys bolivaris*): FMNH 128460.

Provincia de Limón

6. **Cariari, on the Río Tortuguero** (see gazetteer for *O. bolivaris*), 10°22′N/83°31′W, 100 m: LSUMZ 13371–13374.
7. **Suerre** (Goodwin [1946: 457] stated that Suerre is ‘‘a ‘finca’ near Jiménez, altitude about 1500 feet. Alfario's [sic] collecting station.’’ He went on to mention that ‘‘Suerre was also the old name for Llanos de Tortuguero, at the mouth of the Reventazón and principal port of entry for the early colonists.’’), 10°13′N/83°44′W (for Jiménez, USBGN Costa Rica, 1983: 56): AMNH 10781/9080.

Provincia de Cartago

8. **Peralta: Santa Teresa,** 09°56′N/83°47′W (USBGN Costa Rica, 1983: 113): AMNH 141874.

PANAMÁ

Provincia de Bocas del Toro

9. **Sibube,** 09°36′N/82°47′W (Fairchild and Handley, 1966: 13): USNM 335726, 335727.
10. **7 km SSW Changuinola (Risco River),** 09°27′N/82°31′W (for Changuinola; Fairchild and Handley, 1966: 13): USNM 316198–316205.

11. **Almirante,** 09°18′N/82°24′W (Fairchild and Handley, 1966: 13): USNM 316192–316196.
12. **Río Changena,** 09°06′N/82°34′W (Fairchild and Handley, 1966: 13): USNM 319489.
13. **Boca del Drago: Isla Colón; La Gruta,** 09°24′N/82°16′W (Fairchild and Handley, 1966: 13): USNM 316197, 464941–464943, 464945–464947. *Not mapped.*
14. **Cayo Nancy, 7.3 km ESE Bocas del Toro,** 09°19′N/82°11′W (Geographic Names Division, 1969: 233) USNM 464948–464958, 464960, 464961. *Not mapped.*
15. **Isla Bastimentos,** 09°19′N/82°08′W (Fairchild and Handley, 1966: 13). **SE end:** USNM 324184–324191. **Punta Vieja [Old Point]** (09°18′N/82°04′W, Fairchild and Handley, 1966: 13): USNM 335728, 335729, 464399. *Not mapped.*
16. **Isla Popa, 1 km SE Deer Island Channel** (Isla Popa: 09°11′N/82°07′W [Geographic Names Division, 1969: 264], Isla Deer 09°14′N/82°08′W [Geographic Names Division, 1969: 78]): USNM 464401–464410. **Isla Popa, S shore, 1 km E Sumwood Channel (= Sumwood Canal),** 09°09′N/82°09′W (for Sumwood Canal; Geographic Names Division, 1969: 302): USNM 579192–579201. *Not mapped.*
17. **Cayo Agua (Water Keys),** 09°10′W/82°02′W (Fairchild and Handley, 1966: 13): USNM 324192–324235, 32487, 32848, 574957, 578395–578397, 578399, 578459, 578460. **Punta Norte:** USNM 335730, 335731. **Water Keys:** USNM 324847, 324848. **Corozal Lab:** USNM 324849. *Not mapped.*
18. **Península Valiente, Punta Alegre,** 09°05′N/81°51′W (for Península Valiente; Geographic Names Division, 1969: 316): USNM 578400–578409. **Quebrada Hido:** USNM 578461.
19. **Ñurí,** 08°55′N/81°49′W (Geographic Names Division, 1969: 237): USNM 575681–575695.
20. **Isla Escudo de Veraguas,** 09°06′N/81°33′W (Fairchild and Handley, 1966: 13): USNM 307057 (holotype of *Hoplomys gymnurus wetmorei*), 324128–324183, 578392–578394, 578450–578458. **W point**: USNM 579202, 579203. *Not mapped.*

Provincia de Canal Zone

21. **Gatún,** 09°15′N/79°56′W (Fairchild and Handley, 1966: 14): AMNH 36791, 36792, USNM 171239. **near Río Indio,** 09°15′N/79°59′W (Fairchild and Handley, 1966: 14): USNM 170971, 170972 (holotype of *Hoplomys goethalsi*). **Fort Sherman, 6 km W Cristóbal,** 09°21′N/79°57′W (Fairchild and Handley, 1966: 15): USNM 457895–457897. **Camp Piña,** 09°16′N/80°00W (Fairchild and Handley, 1966: 15): USNM 300445, 324961. **3 mi S Fort Sherman, Mohinga Valley,** 09°18′N/79°59′W (Fairchild and Handley, 1966: 14): USNM 296333–296335, 300445.

Provincia de Panamá

22. **“Cerro Azul” (= La Zumbadora**, the “Cerro Azul” of Handley; see gazetteer for *Oryzomys bolivaris*), 09°14′N/79°21′W: USNM 305742–305745, 307005–307014, 310653–310655, 314588.

Provincia de San Blas

23. **Río Cangandi,** 09°26′N/79°07′W (Fairchild and Handley, 1966: 19): USNM 305741.
24. **Armila: Quebrada Venado,** 08°40′N/77°27′W (for Armila; Fairchild and Handley 1966: 19): USNM 335732, 335735–335738. **Río Pito,** 08°40′N/77°26′W (Fairchild and Handley, 1966: 19): USNM 335733, 335734.

Provincia de Darién

25. **Tacarcuna Village,** 08°05′N/77°17′W (Fairchild and Handley, 1966: 17): USNM 310648–310652, 339065. **Tacarcuna,** 08°05′N/77°17′W (for Tacarcuna Village; Fairchild and Handley, 1966: 17), 2650 ft: AMNH 38001–38006. **La Laguna (= Tacarcuna Laguna),** 08°04′N/77°19′W (Fairchild and Handley, 1966: 17): USNM 339064.
26. **Santa Cruz de Cana,** 07°47′N/77°42′W (Fairchild and Handley, 1966: 17): USNM 179033–179035, 179576, 17966.

COLOMBIA

Departamento de Antioquia

27. **Villa Arteaga**, 07°20′N/76°26′W (Hershkovitz, 1977: 925), 130 m: FMNH 70102.
28. **Alto Bonito,** ca. 07°05′N/76°30′W (Paynter and Traylor, 1981: 5), 1500 ft: AMNH 37747.
29. **La Tirana,** ca. 07°21′N/75°03′W (Paynter and Traylor, 1981: 142): USNM 499753–499755.

Departamento del Chocó

30. **Bagadó,** 05°25′N/76°24′W (Paynter and Traylor, 1981: 16): AMNH 34141, 34151.
31. **Río Baudo, Río Sandó (= Quebrado Sandó),** 05°03′N/76°57′W (for Quebrada Sandó; Paynter and Traylor, 1981: 224), 160 m: FMNH 90125–90128.
32. **Río Docampado,** 04°45′N/77°18′W (Paynter and Traylor, 1981: 70), 75 m: FMNH 90115–90121, 90129, 90130. **Río Capico**, 04°40′N/77°15′W (Paynter and Traylor, 1981: 38), 350 m: FMNH 90122–90124.

Departamento del Valle del Cauca

33. **Río Calima, 1 km from San Isidro,** 04°08′N/77°04′W (for Río Calima; Paynter

and Traylor, 1981: 34): USNM 554242, 554243.

34. **6 km N Buenaventura,** 03°53′N/77°04′W: USNM 464975, 554238–554241.
35. **Zabaletas,** 03°44′N/76°57′W (Paynter and Traylor, 1981: 279), 50 m: FMNH 86878. **5 km W Zabaletas, old road to Buenaventura:** USNM 507313.

Departamento del Cauca

36. **Río Saija,** 02°52′N/77°41′W (Paynter and Traylor, 1981:218), 100 m: FMNH 90110–90114.

Departamento de Nariño

37. **Barbacoas,** 01°41′N/78°09′W: AMNH 34209, 34212–34218.
38. **La Guayacana (= Guayacana),** 01°26′N/78°27′W (Paynter and Traylor, 1981: 103): USNM 309042, 309083.
39. **Buenavista,** 01°21′N/78°05′W (Paynter and Traylor, 1981: 28): AMNH 34211.

ECUADOR

Provincia de Esmeraldas

40. **San Javier,** 01°04′N/78°47′W, 60 ft: AMNH 18960; FMNH 29455, 18881 (400 m); USNM 113268–113272.

Provincia del Pichincha

41. **Río Blanco, Mindo** (see discussion in Paynter, 1993: 20), 00°02′S/78°48′W: AMNH 120994.

SIGMODONTOMYS ALFARI

HONDURAS

Departamento de Gracias a Dios

1. **Río Coco,** 14°45′N/84°03′W (Pine 1969: 643): USNM 392876, 392877.

NICARAGUA

Departamento de Matagalpa

2. **Río Tuma** [‘‘near the present village of Sardinal, Matagalpa (13°03′N/85°35′W),’’ as determined by Jones and Engstrom, 1986: 20], 500 ft: AMNH 29555.
3. **Río Grande, S of Tuma** (This place, according to Jones and Engstrom, 1986: 20, is ‘‘evidently . . . on the Río Grande [de Matagalpa] near the mouth of the Río Upa, approximately equidistant between two of Richardson’s other stations–Muy Muy and Uluse.’’ They emphasize that some researchers have erroneously placed it in Departamento de Zelaya.), 700 ft: AMNH 28547, 28548 (holotype of *Oryzomys ochraceus*), 28549, 28550.
4. **Hacienda Tepeyac** (also called Finca Tepeyac, which Jones and Engstrom, 1986: 7, place at ‘‘10.5 km N, 9 km E Matagalpa, 960 m’’): USNM 337584.

Departamento de Zelaya

5. **Río Kurinwas,** 12°52′N/84°05′W: USNM 392875.

COSTA RICA

Provincia de Alajuela

6. **Seven km by road NE Villa Quesada** (see gazetteer for *O. bolivaris*), 10°19′N/84°26′W, 700 m: LSUMZ 29267.

Provincia de Cartago

7. **Peralta, El Sauce** (Goodwin, 1946: 457, described El Sauce as ‘‘a farm on the Atlantic railroad, near Perálta, altitude 1000 feet,’’ 09°58′N/83°37′W (for Peralta; USBGN Costa Rica, 1983: 87): AMNH 123305, USNM 250223, 250224.
8. **Peralta, Santa Teresita** (?= Santa Teresa; Goodwin, 1946: 457 described a Santa Teresa and did not mention any Santa Teresita. USBGN for Costa Rica [1983: 113] lists only one Santa Teresita, but it is in Provincia de Puntarenas), 09°56′N/83°47′W (for Santa Teresa; USBGN Costa Rica, 1983: 113): AMNH 141887.

Provincia de Limón

9. **Cariari, on the Río Tortuguero** (see gazetteer for *O. bolivaris*), 10°22′N/83°31′W, 100 m: LSUMZ 13188, 13200.
10. **Jiménez, 3 mi E Guápiles,** 10°13′N/83°44′W (USBGN Costa Rica, 1983: 56), 700 ft: AMNH 12436/10744 (holotype of *Sigmodontomys alfari*).
11. **Estrella Valley, Pandora,** 09°43′N/82°57′W (McPherson, 1985: 262): USNM 284658.

PANAMÁ

Provincia de Bocas del Toro

12. **Almirante,** 09°18′N/82°24′W (Fairchild and Handley, 1966: 13): USNM 315996–316005.
13. **Río Changena,** 09°06′N/82°34′W, 2400 ft: USNM 319488.
14. **Tierra Oscura,** 09°11′N/82°17′W (Geographic Names Division, 1969: 306): USNM 449896.
15. **Isla San Cristóbal; Bocatorito,** 09°14′N/82°16′W (Geographic Names Division, 1969: 27): USNM 449895. *Not mapped.*
16. **Ñurí,** 08°55′N/81°41′W (Geographic Names Division, 1969: 237): USNM 575661, 575662.

Provincia de Chiriquí

17. **Boquerón,** 08°31′N/82°34′W (Fairchild and Handley, 1966: 15): AMNH 18802.

Provincia de Veraguas

18. **Santa Fé,** 08°31′N/81°04′W (Fairchild and Handley, 1966: 20): USNM 304813.

Provincia de Coclé

19. **6 mi E El Valle,** 08°36′N/80°08′W (for El Valle): USNM 304799.

Provincia de Canal Zone

20. **Fort Sherman, 6 km W Cristóbal,** 09°21′N/79°57′W (Fairchild and Handley, 1966: 15): USNM 457332, 457333.
21. **Summit,** 09°03′N/79°40′W (Fairchild and Handley, 1966: 15): USNM 396465.

Provincia de Panamá

22. **Campana Hill (= Cerro Campana),** 8°41′N/79°56′W (Fairchild and Handley, 1966: 18), 3000 ft: USNM 298713–298715.
23. **''Cerro Azul'' (= La Zumbadora**, the ''Cerro Azul'' of Handley; see gazetteer for *Oryzomys bolivaris*)**,** 09°14′N/79°21′W: USNM 302492, 305717, 306963–306969, 310597, 314582.

Provincia de San Blas

24. **Mandinga,** 09°29′N/79°05′W (Fairchild and Handley, 1966: 19): USNM 305715, 305716.

Provincia de Darién

25. **Tacarcuna,** 08°07′N/77°14′W (Fairchild and Handley 1966: 17), 2650 ft: AMNH 37900–37914. **Tacarcuna Village,** 08°05′N/77°17′W (Fairchild and Handley 1966: 17), 3200 ft: USNM 310585–310596.
26. **Paya,** 07°53′N/77°24′W (Fairchild and Handley, 1966: 17): USNM 310487.
27. **Santa Cruz de Cana,** 07°47′N/77°42′W (Fairchild and Handley, 1966: 17), 1800 and 2000 ft: USNM 178622–178626, 178627 (holotype of *Nectomys alfari efficax*), 178628–178637, 178639–178641, 178677, 178977.
28. **Jaqué; junction of Ríos Jaqué and Imamado,** 07°31′N/78°10′W (for Jaqué and Río Jaqué; Fairchild and Handley, 1966: 17): USNM 363183–363185.

VENEZUELA

Estado de Zulia

29. **Novito, 19 km WSW Machiques** (on lower eastern ''slopes of Sierra de Perijá, overlooking valley of Río Negro,'' Handley, 1976: 77), 10°02′N/72°43′W, 1155 and 1134 m: USNM 442251, 442252. *Not mapped.*

COLOMBIA

Departamento de Norte de Santander

30. **San Calixto; Río Tarra,** 08°39′N/73°01′W (USBGN Colombia, 1988): USNM 279742–279745. *Not mapped.*

Departamento del Chocó

31. **[Gorgas Memorial Laboratory], Río Truando, Teresita,** 07°26′N/77°07′W: FMNH B-000185, B-863.

Departamento de Antioquia

32. **Valdivia,** 07°11′N/75°27′W (USBGN Colombia, 1988: 825), 1200 m: BMNH 98.10.3.13 (holotype of *Nectomys russulus*).
33. **La Tirana,** ca. 07°21′N/75°03′W (Paynter and Traylor, 1981: 142), 520–670 m: USNM 499608 (taken from snake), 499611–499616. **Aljibes, 1 km S La Tirana,** 630 m: USNM 499609, 499610.

Departamento del Valle del Cauca

34. **Buenaventura, Palmares del Pacifico,** 03°'53′N/77°04′W (for Buenaventura; Paynter and Traylor, 1981: 27): USNM 483981.
35. **Río Raposo, Virology Field Station,** ca. 03°38′N/77°05′W (for Raposo; Paynter and Traylor 1981: 211): USNM 334703–334708.

Departamento del Cauca

36. **Güengüé,** ca. 03°14′N/76°21′W (Paynter and Traylor, 1981: 104): AMNH 32183.
37. **Sabanetas,** 02°32′N/76°53′W (Paynter and Traylor, 1981: 217), 1900 m: FMNH 90282.

Departamento de Nariño

38. **Barbacoas,** 01°41′N/78°09′W: AMNH 34191, 34192; 75 ft: AMNH 34193 (holotype of *Oryzomys barbacoas*).
39. **La Guayacana (= Guayacana),** 01°26′N/78°27′W (Paynter and Traylor, 1981: 103), 200 m: FMNH 89563.

ECUADOR

Provincia de Esmeraldas

40. **San Javier,** 01°04′N/78°47′W, 60 ft: BMNH 1.3.19.8 (type of *Nectomys esmeraldum*), 1.3.19.9, 1.3.19.10, 1.8.3.4; USNM 113295, 113298, 113299.
41. **''Ecuador, west of Quito''** (This is the locality given by Thomas [1921: 449], who described *ochrinus*. Hershkovitz [1948: 54] wrote that the ''type of *ochrinus* is . . . quite like the specimens recorded by the writer from Carolina, Río Mira, Ecuador. The original specimen of *ochrinus* 'collected' by Söderström from 'west of Quite' could very well have originated in the Río Mira region on the western slope of the Cordillera Occidental.''): BMNH 21.2.15.4 (holotype of *Oryzomys barbacoas ochrinus*). *Not mapped.*

Provincia del Pichincha

42. **Río Blanco, near Mindo** (see discussion in Paynter, 1993: 20), 00°02′N/79°48′W, 4000 ft: BMNH 34.9.10.214.

Provincia del Chimborazo

43. **Puente de Chimbo** (02°10'S/79°06′W, for Bucay; see gazetteer for *Oryzomys talamancae*), 1200 ft: AMNH 63342.

Provincia del Guayas

44. **Bucay,** 02°10'S/79°06′W (Paynter, 1993: 23), 1000 ft: AMNH 61355.

APPENDIX I

The Original French Translation of Azara’s (1801: 82–85) Description of ‘‘Rat Second, ou Rat à Grosse Tête’’

Rat Second, ou Rat à Grosse Tête

Cette espèce paroît nouvelle.

Il n’a point de nom-propre, et je n’en sais point qui puisse mieux caractériser cet animal que celui que je lui donne.

Deux Indiens du village de Saint-Ignace-Gouazou (*a*) me vendirent, à des jours différens, deux femelles semblables entre elles, sans me donner d’autres renseignemens, si ce n’est qu’ils les avoient prises dans leurs *chacarras*, ou la charrue avoit mis à découvert la retraite de ces animaux. Je les comparai avec un Rat commun, que je tins présent pour cet effet, et il me parut que ces deux femelles étoient adultes.

Longueur, 8 pouces (21 centimètres 3 cinquièmes).

Queue, 4 pouces (11 centimètres) toute pelée, excepté dans 3 lignes (6 millimètres) prises à sa racine; peu grosse à sa naissance, et uéanmoins elle ne diminue pas avec autant de rapidité que dans le Rat ordinaire, jusqu’à sa pointe qui est aiguë.

Quoique toutes les formes de cet animal soient celles du Rat, il a la tête beaucoup plus grosse et plus courte; l’oeil est plus petit et moins saillant; l’oreille est beaucoup plus courte, longue de 6 lignes (1 centimètre 1 tiers) au-dessus de la tête; large de 6 lignes (1 centimètre 1 tiers) aussi, et plus ronde; les moustaches sont beaucoup plus minces et plus courtes; les joues sont plus grosses, et si avancées en-dehors, qu’elles rendent la tête presque aussi large que le corps; la distance est moindre entre les yeux, et plus grande entre les oreilles que dans le Rat. Les jambes de derrière, comparativement à celles de devant, sont plus longues; le tarse principalement est beaucoup plus grand, et il est long de 13 lignes (3 centimètres), y compris l’ongle; la queue est plus grèle, moins nerveuse, et elle naît d’une croupe moins obstuse.

Dans la patte de devant, il y a les mêmes quatre doigts et le même rudiment de pouce que dans le Rat, avec une semblable disposition; une pareille identité se montre dans les doigts du pied de derrière.

Du museau à la queue, l’animal est brun; les côtés du corps et ceux de la tête lesont aussi, mais plus clairs, et avec un peu de nuance cannelle. En dessous, tout est blanchâtre, tirant un peu sur le cannelle.

Trois jours avant, un Indien du même village m’avoit vendu un Rat, pris dans son *chacarra*, et me dit que ce petit animal alloit avec quatre autres qui lui étoient égaux en grosseur, et encore avec un autre plus grand, mais qu’ils avoient tous échappé. Cette circonstance me fit croire que celui que j’achetois n’étoit point adulte, quoique ses testicules me parussent très-gros pour ceux d’un individu jeune. Je le décrivis, ayant devant moi un petit Rat commun.

Il étoit long de 5 pouces (13 centimètres et demi); et comme la queue étoit proportionnée à celle du Rat à grosse tête, que j’ai décrit cidessus, et que toutes leurs formes étoient semblables, je ne doutai point que ce ne fût un petit de l’espèce actuelle; et en conséquence ie place ci-après la comparaison que j’ai faite de ce petit Rat à grosse tête, avec le petit Rat commun.

Le jeune Rat *à grosse tête*, a la tête beaucoup plus grosse, et la distance entre les oreilles est plus grande; la face n’est pas aussi plate, et le museau n’est ni aussi aigu, ni aussi long, ni aussi effilé.

Le poil, depuis le nez jusqu’au haut de la tête, n’est pas aussi couché; les moustaches sont plus courtes, moins saillantes en-dehors.

L’œil et l’oreille sont plus petits; cette dernière est plus étroite, épaisse, droite et a quelques petits poils en dedans; elle passe la tête de 4 lignes (9 millimètres); elle est large de plus de 3 lignes (6 millimètres), et ronde à son extrémité.

La queue est plus menue à sa racine, et naît d’une croupe moins arrondie.

Les testicules sont ceux du Rat commun, longs de 4 lignes (9 millimètres), gros de 2 lignes (plus de 4 millimères).

Toute la partie inférieure est blanchâtre, et n’a pas le reflet bai du petit Rat commun, et toute la partie supérieure et les côtés, sont d’une nuance plombée, plus obscure que dans le petit Rat commun.

(*a*) Placé à environ 34 lieues et demie (19 myriamètres) dans le Sud-quart-Sud-Est de la cité de l’Assomption. (*Note du Traducteur*).

APPENDIX J

Lund's (1840 preprint of 1841 text: 279–280) Description of *Mus laticeps* in the Original Danish

Den anden Afdeling, hvor Halen er kortere end Legemet, indeholder ei saa store Arter, som den förste. Den förste er *Mus laticeps*, 10″ 5‴ lang, hvoraf legemet 5″ 5‴, Halen 5″, udmærket ved sit brede og höie Hoved, store Ören, fremspringende Öine og meget fine Hale. Dens Farve er oven lys-askergraa med stærk Indblanding af rustguult, unden reen hvid.

APPENDIX K

Winge's (1887: 48–50) Description of *Calomys saltator* in the Original Danish

23. *Calomys saltator* nomine novo[5]) (Pl. I, fig. 16, 17; Pl. III, fig. 7).

Nulevende ved Lagoa Santa (hjembragt er 1 i Spiritus, 1 Skelet, 4 Skind), men hidtil ikke med fuld Sikkerhed funden i Ugleglyp fra nyeste Tid eller jordfunden.

Dens nærmeste Slægtninge ere snarest *C. longicaudatus* og *C. plebejus*; men den har adskillige Egenheder.

Fra *C. laticeps* afviger den i følgende:

Ydre. Øret er større; Fligen paa Ørets Forrand næppe synlig; *Antitragus* næsten ikke fremstaaende. Hænderne betydelig længere og smallere; Trædepuderne større og meget spidst fremstaaende; Huden mellem Trædepuderne tavlet-grynet; alle Ringene paa Fingrenes Underside tydelige: 7, 7, 7, 6. Foden længere og smallere, de tre mellemste Tæer især længere; Trædepuderne iøjnefaldende spidst fremstaaende; Huden mellem Trædepuderne grynet-tavlet; Ringene paa Tæernes Underside fuldstændige: 4, 9, 10, 9, 6.

Ørets Haarklædning over det meste meget svagere, med kun korte spredte Haar, saa at den nøgne Hud ses meget; kun et skarpt afgrændset Stykke af Ydersiden af *Helix* forrest er tæt klædt med samme bløde Haarklædning som Issen. Legemets Haarklædning meget kortere og blødere, de enkelte Dækhaar finere. Paa hele Oversiden, ogsaa paa Hovedet, er der færre af de sorte Haar, og de gullige Haar nærme sig i Farven til Gulbrunt; i Aftstand er Oversiden derfor mere ensfarvet gulbrun.

Maal af et Exemplar i Spiritus (1.), ♀:

Krop	120.
Hale	127.
Snude til forreste Øjekrog	16½.
Forreste Øjekrog til Øre	17½.
Snude til Øre	32.
Mellem de forreste Øjekroge	11.
Mellem de bageste Øjekroge	15.
Mellem Ørene	11½.
Øjeæblets vandrette Tværmaal	5¼.
Ørets Længde	19½.
Ørets Brede	15½.
Hovedets Højde foran Øret	18.
Snudens Højde bag Fortænderne	9½.
Hovedets Længde	38.
Hovedets Brede foran Ørene	18½.
Albue til Haandled	23.
Haandled til Spidsen af 1ste Finger	6⅓.
– – – – 2den –	12.
– – – – 3dje –	14⅓.
– – – – 4de –	13½.
– – – – 5te –	10½.
Haandrodens Brede	3⅔.
Knæ til Hæl	36.
Hæl til Spidsen af 1ste Taa	21³⁄₃.
– – – – 2den –	29¾.
– – – – 3dje –	31.
– – – – 4de –	30½.
– – – – 5te –	25½.
Fodrodens Brede	4¾.
Negl paa 3dje Finger	1¾.
Negl paa 3dje Taa	3.
Længste Varbørste	44.
Haarene paa Halespidsen	1½.

Maal af Skind:

	2. ♀	3. ♂	4. ♀
Krop	146	135	123.
Hale	c.139	c.125	105.
Fod	29½.		

Tænder. Den nedre Fortand frembringer med sin bageste Ende næsten ingen Udposning paa Underkjæbens Yderside. Ellers kan der i Tænderne næppe paavises nogen fast Forskjel.

Hovedskal. Hjernekassen er mindre i Forhold til Ansigtet. Panden fortil lidt tydeligere nedhulet. Ingen *Prc. supraorbitalis*; Pandens Øjehulerand skarp. *Foramen opticum* betydelig mindre, tildels fordi noget er forbenet af den Hinde, der ellers delvis udfylder det. Ingen Fontanelle i Næsegangens Sidevæg mod *Fissura orbitalis*. *Prc. post-tympanicus* er bagtil togrenet; men Indsnittet er ikke stort. *Foramen incisivum* meget kortere, naar mindre langt frem og mindre langt tilbage. Oftest kun svag Antydning til Grube omkring det bageste *Foramen palatinum*. Trommebenet usædvanlig lille og fladt, dækker mindre af *Foramen lacerum anterius*. En lille Fontanelle i *Pars mastoidea*. *Tegmen tympani* lidt længere, rører ved *Sqvama*, men lægger sig dog heller ikke pladeformet udenpaa bageste Rand af *Sqvama*. Underkjæben har ingen særskilt udstaaende Pukkel efter Fortandens bageste Ende. *Prc. coronoideus* har mere skraanende Forrand. Issebenet har næsten ingen Plade paa Hjernekassens Side.

Maal af den afbildede Hovedskal (2.), ♀ ad., og af andr:

Øvre Kindtænders Række	5¼.
Nedre Kindtænders Række	5¼.
Øvre Fortænders samlede Brede	2.
Længden af *Basioccipitale*	5.
Længden af bageste Kilebenskrop	5.
Mellem Spidserne af *Prc. jugulares*	8.
Breden af bageste Kilebenskrop bagest	2¾.
Længden af Trommebenet	3⅓.
Mellem *Prc. ectopterygoidei*	8.
Ganens Brede mellem begge *m* 2	3½.
Længden af *Foramen incisivum*	4⅔.
Højden af Ydervæggen af *Canalis infraorbitalis*	6.
Hovedskallens Længde	30½.
Fra øvre *m* 1 til Fortand	8⅔.
Fra nedre *m* 1 til Fortand	4⅓.
Næsebenets Længde	13.
Længden af Sømmen mellem Pandebenene	10¾.
Længden af Sømmen mellem Issebenene	5½.
Pandens Brede mellem Øjehulerne	5⅓.
Pandens Brede over *Sutura coronalis*	10⅓.
Ansigtets Brede over Kindbuerne	17⅔.
Hjernekassens Brede over Øreaabningerne	13.
Underkjæbens Længde	18.
Underkjæbens Højde under *m* 1	4¾.

	5. ad.	3. ♂ ad.	1. ♀ ad.
Øvre Kindtænders Række	5	5	5.
Hovedskallens Længde	31⅔		30.
Fra øvre *m* 1 til Fortand	9	8½	8⅓.
Længden af *For. incisivum*	4¾	4½	4⅔.
Næsebenets Længde	13⅔	13	13.
Underkjæbens Længde	18⅔	17⅓	18.

Det øvrige Skelet (ikke alle Hvirvler kjendes). De lange Lemmeknogler ere gjennemgaaende lidt sprinklere. Overarmens *crista supinatoria* er svagere og *Condylus internus* mindre fremstaaende. *Tibia* lidt længere.

Maal af et Skelet (5), hvis Hovedskal er 31⅔$^{\text{mm}}$lang:

Skulderblad	16.
Overarm	18⅔.
Ulna	23⅔.
Bækken	28.
Laarben	27½.
Tibia	31.

APPENDIX L

Winge's (1887: 151) Footnote 5, Part 10, in the Back of His Report on Rodents from Lagoa Santa, in the Original Danish

10) *Calomys saltator* er et nyt Navn givet til den ene af de to Arter, der have været sammenblandede under Navnet *Hesperomys laticeps* Lund. Lund's Originaler til *laticeps* ere begge af en Art, den, der her er kaldt *saltator*; men Lund har dog næppe selv opfattet Arten skarpt; Reinhardt, der ogsaa samlede Mus under sit Ophold hos Lund i Lagoa Santa, og som vistnok har raadført sig med Lund om Navnene, har i hvert Fald brugt Navnet *laticeps* (paa Etiketter) for an anden Art, en Farve-Varietet af *H. vulpinus* Lund. — Ogsaa Burmeister har brugt *laticeps* for *vulpinus* Lund; at dette Tilfældet, kan egenlig ikke ses af Burmeisters Beskrivelse; dertil er den altfor lidt karakteriserende; men Giebel (Beitr. Osteol. Nageth., pl. V, f. 6) har afbildet Hovedskallen af Burmeister's Exemplar af ⟨⟨*laticeps*⟩⟩ fra Lagoa Santa (Giebel: Zeitschr. ges. Naturw., Bd. 28, 1866; p. 120), rigtignok meget unøjagtig og under Navn af *H. subflavus* Wgnr., og Giebel's Afbildning forestiller Lund's ⟨⟨*vulpinus*⟩⟩. (Burmeister mente, at Wagner's *H. subflavus* var den samme son ⟨⟨*laticeps*⟩⟩; men dette er alt andet end sikkert og kan ikke afgjøres uden Eftersyn af Originalen.) — Navnet *vulpinus* Lund kan ikke holdes, fordi det har været brugt tidligere for en anden Art, *H. vulpinus* Licht. — Under disse Omstændigheder er det sikkert rigtigst at lade Navnet *laticeps* blive ved den Art, hvis Hovedskal Giebel har afbildet, og paa hvem det passer, og give det nye Navn, der er nødvendigt, til den anden af de to sammenblandede Arter.

Hvad Thomas (P. Z. S. 84) mener med ⟨⟨*Hesperomys* (*Oryzomys*) *laticeps* Lund⟩⟩, kan man ikke se.

Prof. Leche mener, at der imellem Mus fra Syd-Brasilien findes nogle, der, i det mindste hvad Hovedskallen angaar, gjøre Overgang mellem *C. laticeps* og *C. saltator*; en Syd-Brasilianer har han bestemt som ⟨⟨*Hesperomys laticeps* var. *intermedia*⟩⟩; han havde fra Kjøbenhavns Museum laant Hovedskaller af baade *laticeps* og *saltator* til

Hjælp ved Bestemmelsen. Leche opfører tre Forskjelligheder mellem *laticeps* og *saltator*: 1) i Formen af Pandens Øjehulerand; heri er hans var. *intermedia* allernærmest ved *laticeps*; 2) i Størrelsen af *Foramen incisivum*; ogsaa heri er *intermedia* omtrent som *laticeps*; i Længden af *F. incisivum* er der hos *laticeps*, som hos saa mange andre Mus, betydelige individuelle Forskjelligheder; men saa ejendommelig kort og bredt, som det altid er hos *saltator*, er det aldrig hos *laticeps*; 3) i Formen af Næsebenet, hvori *intermedia* skal være undertiden som *laticeps*, undertiden som *saltator*; men i denne Henseende er der ingen Forskjel mellem *laticeps* og *saltator*; Næsebenets Form bagtil er hos begge temmelig stærkt individuelt forskjellig, som saa ofte hos Mus. Men Prof. Leche har overset de fleste og tildels vigtigste Forskjelligheder mellem Hovedskallerne af *laticeps* og *saltator*; Forskjellen i Trommebenet, i Næsegangens Væg og i den bageste Ende af den nedre Fortands Grube, og Arternes Ydre kjender han ikke, altsaa ikke Forskjellen i Øre, i Hænder og Fødder (om Forskjellen i Fødder havde jeg skriftlig sagt ham et Par Ord som Begrundelse af Navnet *saltator*), o.s.v. I Virkeligheden ere *laticeps* og *saltator* to af de mest forskjellige *Calomys*-Arter. Hvad Leche's *H. laticeps* var. *intermedia* er, kan man af Beskrivelsen og Afbildningerne ikke se; maaske er det virkelig *laticeps*; *saltator* er det ikke.

APPENDIX M

Transliteration of Burmeister's (1854: 171–172) Description of *Hesperomys laticeps* Lund in the Original German

7. Hesperomys laticeps *Lund*.

Blik p. Bras. Dyr. III. Till. 279.
H. subflavus Wagn. Schreb. Suppl. III. 534. 24.

Oben hell goldgelb, stark mit schwarzbraun gemischt, Nase und Stirn grauer; unten hell isabellgelb, grau durchscheinend. Ohren sehr groß. Schwanz so lang wie der Körper, jeder von beiden 5½–6″.–

Völlig wie die vorige Art gestaltet, ebenso voll und weichhaarig, aber etwas kleiner, der Schwanz kürzer, die Ohren größer, die Farbe helleren Tones. Vorderkopf von der Nase bis hinter die Augen weißgrau, mit vielen schwarzen Haaren gemischt; von da an die ganze Rückenseite hellgelbgrau, eine Mischung aus gelben und schwarzen Haarspitzen, unter denen einzelne längere schwarze Grannen mit seiner weißer Spitze stehen; in der Tiefe alle Haare hell schiefergrau. Kehle weiß, die Seiten gegen die Backen hin isabellgelb, die Brust vor den die Armen gelblich, dahinter graulich. Die Mitte des Bauches und die Weichen weiß, nach außen gelblich, die Farbe am lebhaftesten in der Schenkelfuge am Steißrande und an den Bauchseiten. Schwanz ziemlich dicht behaart, oberhalb braun, unten mehr gelblich. Ohren groß, breit, abgerundet, grauschwarz behaart, innen mit gelblichen Haarspitzen, besonders vorn und am Umfange. Schnurren reichlich, aber sein, etwas über das Ohr hinaus reichend; die meisten schwarzbraun mit weißlicher Spitze. Lippen und Pfoten weiß. Die Arme und Beine außen wie der Rücken gefärbt, nur matter, die Sohle nackt, fleischfarben; die Schneidezähne vorn hellgelb. — Ganze Länge 11–12″, Kopf und Rumpf 5½–6″, der Schwanz 6″, Kopf bis zum Ohr 1″5‴, Ohr innen 8‴, Hinterpfote 14‴. — Von Lagoa santa.

Anm. Unter den von Dr. Lund kurz definirten Mäusen derselben Gegend (a.a.O.) paßt der Mus laticeps gut hierher, aber dessen Dimensionen sind um 1½″ im Rumpf und Schwanz kleiner angegeben. Von den beiden mir vorliegenden Bälgen hat der kleinere einen relativ etwas längeren Schwanz; beide sin Männchen. Wagner's Beschreibung ist kenntlich und läßt über die Identität seiner Art mit meinen Examplaren keinen Zweifel. — Nahe verwandt damit ist Azara's Cola igual al Cuerpo (Quadrup. II. 87. No. 87. — Trad. franc. II. 82. — Mus cephalotes *Desm.* Mamm. 305. — *Brants* Muiz. 144) aber kleiner (Körper 4″, Schwanz 4″) und heller grau, rothbraun melirt, unten weiß. —

APPENDIX N

Brants' (1827: 139–141) Description of *Mus physodes* in the Original Dutch

53. (26) M. PHYSODES Licht. *De drievingerige rat.*

Schoon roodbruin op den rug, helder-wit aan de onderzyde, beide kleuren scherp afgezonderd, slechts drie duidlyke vingers aan de voorvoeten.

Maten:

Lengte van de neus tot aan de staart	6	*duim*	8	*lyn.*
– *der staart*	5	–	9	–
– *der kop*	1	–	5	–
– *der ooren*	–	–	6	–
– *der achtervoeten*	1	–	4	–

De kleur is over de gansche bovenzyde van het ligchaam en kop vry eenvormig, roodbruin met veele zwarte langere haarspitsen gemengd, welke op het midden der rug vooral, tusschen de andere uitsteken, de onderzyde, de binnenzyde der ledematen, de voeten en handen en onderste helft der bovenlip byna tot aan de oogen, zyn van eene helder witte kleur, die snel van de roodbruine der bovenzyde afgescheiden is. Het haar zelve is zeer zacht, glanzend en aanliggend, leikleurig aan zynen oorsprong. Het ligchaam is langstrekkig , het hoofd middelmatig en puntig, de ooren wit van kleur, naakt en vry groot, de gehooropening duidlyk zichtbaar, de neus is vooruitstekend met eene sterke haarkam bezet, de bovenlip gespleten, de snytanden smal en gekleurd, de voeten met eene schubbige huid bedekt. De voorste hebben slechts die duidelyke vingers, het stompje der duim zeer hoog geplaats draagt geen wel gevormden nagel meer. De kleine vinger, is desgelyks niets meer dan een byna onmerkbaar stompje, draagt echter eenen ten uiterst kleinen, doch welgevormden nagel, de achtervoeten hebben vyf vingers en even als de voorvoeten witte gekromde nagels, de vingers met lange witte haren bedekt. De staart wit, byna naakt, van middelmatige lengte. Over het algemeen is de gedaante van dit dier zeer langstrekkig en niet onbevallig; haar vaderland is Brasilien.

Het Berlynsch Museum en het Brasiliansche te Weenen bezitten exemplaren van hetzelve.

APPENDIX O

Lichtenstein's (1830) Description of *Mus physodes* in the Original German

XXXIV$^{\text{ste}}$ Tafel.
1$^{\text{ste}}$ Figur.
MUS PHYSODES LICHT.
Die dreizehige Ratte.

Artkennzeichen: Größe einer jungen Hausratte, mit langen Hinterfüßen, langem Schwanz, großen nackten Ohren, nur drei deutlichen Zehen an den Vorderfüßen, oben gelbbraun, unten rein weiß.

Maaße:

Ganze Länge von der Schnauze bis zur Schwanzwurzel	7	Zoll	–	Lin.
Länge des Schwanzes	6	”	–	”
” ” Kopfes bis zum Nacken	2	”	–	”
” der Ohren 7 Lin.; Breite derselben	–	”	6	”
” des Hinterfußes vom Hacken bis zur Krallenspitze	1	”	5	”

Das Haar ist ziemlich straff doch dicht, auf der Haut hellgrau, nach außen gelbbraun und auf dem Rücken mit braunen Spitzen. An den Seiten sondert sich die rothbraune Farbe in gerader Linie vom Knie bis Ellenbogen scharf von der rein weißen Bauchseite. Auch die vier Füße, so wie die Unterseite des ganz nackten Schwanzes, sind weiß. Die Außenzehe der Vorderfüse ist bis auf ein kurzes Stümpfchen mit kleinem rundlichem Nagel, verschwunden. Von den drei übrigen Zehen sind die beiden äußeren fast gleich lang, die innere ansehnlich kürzer. Der Haarkamm ist hoch, die Bartborsten sind länger als der Kopf, sehr fein und von brauner Farbe.

Mit Azara's *Anguya* (*) ist diese Art nahe verwandt, doch abweichend in der weniger lebhaften Färbung, den nicht genug zutreffenden Maaßen und der, wenigstens von Azara nicht erwähnten, Dreizehigskeit.

Ihr Fundort ist die Provinz San Paulo Brasiliens.

(*) *Apuntamiento para la historia natural de los quadrupedos del Paraguay*. Tom. II. No. 48 — Traduction françoise. Tom. II. pag. S6.

APPENDIX P

Transliteration of Burmeister's (1854: 167) Description of *Hesperomys physodes* in the Original German

4. Hesperomys physodes *Licht*.

Wagn. Schreb. Suppl. III. 535. 26.
Mus physodes *Brants* Muiz. 139. 53. — *Lichtenst*. Darst. n. Säugeth. etc. Taf. 34, Fig. 1.
? Hesper. russatus *Wagn*. Münch. Acad. Abh. V. 312. 6.

Hell zimmtbraun auf der Oberseite, rein weiß am Bauch, beide Farben scharf einander abgesetzt; der nackte Schwanz etwas kürzer als der Körper; dieser 6⅔″, jener 6⅓″.

Sehr zierlich und fein gebaut, besonders die Pfoten und der Schwanz, aber die Ohren groß. — Das Haarkleid weich, kurz, knapp anliegend, aber doch sanft anzufühlen. Ganzer Rücken von der Schnauße bis zum Schwanz hell rothgelbbraun, eine Mischung der Zimmtfarbe mit Orange; die Backen ebenso, aber die Oberlippe und die Halsseiten hinter den Backen weiß; die Beine außen ganz zimmtroth, innen weiß, wie die Pfoten und Zehen; das Weiße überall scharf abgesetzt vom zimmtrothen Theil. Jedes Haar in der Tiefe schön bleigrau, das Ende zimmtroth, oder weiß; die Rückenhaare z. Th. mit dunkleren, braunen Spitzen, die den eingestreuten sehr feinen, kurzen, wenig vom übrigen Pelze unterscheidbaren Grannen angehören. Rasenrücken mit einem Haarkamm; Ohren groß, bauchig gewölbt, abgerundet, innen nackt, am Umfange behaart, besonders an der Borderseite, rothbraun, vor der Spitze auf der hintern Seite ein weißer Fleck. Schnurren fein, braun, die untern weiß. — Pfoten zierlich, die vorderen schmal, wegen des sehr kleinen, aber doch nicht ganz fehlenden Daumens, die Außenzehe ebenfalls sehr klein, aber vorhanden; die 3 mittleren sehr ungleich, die innere stark, die äußere mäßig verkürzt. Hinterpfoten etwas weniger verschmälert, die Zehen frei, verhältnißmäßig lang, die 3 mittlern von fast gleicher Länge, indem die mittelste nur wenig vorspringt. Sohle nackt, fleischfarben, minder deutlich chagrinirt, die Zehen unten fast glatt. Schwanz sehr dünn, höchst sein beschuppt, schwach behaart, wenig gefärbt. — Ganze Länge 13″, Rumpf 6″8‴, Kopf bis zum Ohr 1″5‴, Schwanz 6″4‴, Ohr 7‴, Hinterpfote 1″4‴. — St. Paulo.

Anm. Ich habe das mir von Berlin zur Ansicht gesandte Originalexemplar genau beschrieben; von G. R. Lichtenstein und noch mehr von Brants ist der Schwanz zu kurz angegeben; indem die ½″ behaarte Strecke nicht richtig beim Messen vom Körper getrennt worden. Die Art schließt sich zunächst an Hol. leucogaster *Brandt*, und an Hesp. russatus *Wagn*. a.a.O. Der gelbliche Anflug des Bauches und die lebhafte Farbe auf dem Rücken werden für letzteren als Unterschiede hervorgehoben. —

APPENDIX Q

Wagner's (1848: 312) Description of *Hesperomys russatus* in the Original German

6. *Hesperomys russatus* Wagn. Die goldfalbige Scharrmaus.

H. supra splendide fulvus, subtus albido-lutescens, pedibus albidis; cauda corpore paululum breviore, squamata, nudiuscula, pallida, supra infuscata.

Die Oberseite ist lebhaft goldig pomeranzenfalb, mit wenig Schwartz bespritzelt, an den Seiten etwas lichter. Die Unterseite ist abgeschnitten und schön gelblichweiss, was am Halse und auf der Innenseite der Hinterbeine am blassesten ist. Die Füsse sind schmutzig weiss behaart, die Sohlen nackt. Die Ohren haben einen feinen Haaranflug, der Schwanz ist fast nackt, blass, auf der Oberseite dunkler.

Körper	6″	4‴	Ohren	0″	7½‴
Schwanz	5	9	Hinterfuss	1	5

Es kommt diese Scharrmaus, die *Natterer* von Ypanema mitbrachte, mis *Mus physodes Lieht* so sehr überein, dass sie nur durch die lebhaftere Färbung und den gelben Anflug der Unterseite und der Schnautzenspitze von letzterem, der blos nach dem einzigen Exemplare in Berlin gekannt ist, unterschieden zu seyn scheint. Da beide überdiess gleiche Heimath theilen, so dürften sie wohl nur als Farbenabänderungen einer und derselben Art anzusehen seyn.

APPENDIX R

Leche's (1886: 693–694) Description of *Hesperomys laticeps* Burmeister var. *intermedia* var. nov. in the Original German

H. laticeps Burmeister var.
intermedia var. nov., Fig. 5–8

''*H. darwinii?*'' Hensel 1. c. pag. 48, Fig. 22 non *Mus darwinii* Waterhouse, Voyage etc. pag. 64 (teste Thomas).

Die 9 von v. Jhering gesammelten Exemplare stimmen volkommen mit dem von Hensel als ''*H. darwinii?*'' bezeichneten Schädel überein. Dagegen theilt mir Thomas mit, dass sie nicht mit Waterhouse's *Mus darwinii* identisch sind, welche letztere eine *Phyllotis*-Form ist, während die vorliegenden (ebenso wie Hensel's ''*H. darwinii?*'') jedenfalls zu *Oryzomys* gehören und der *H. laticeps* Lund[1]) nahe stehen. Auf mein Ersuchen hatte Herr Cand. mag. H. Winge die Güte, mir aus dem Zoologischen Universitätmuseum zu Kopenhagen 3 Schädel zu senden, von denen zwei (von Lund selbst gesammelt) als *H. laticeps* Lund–Burmeister, der dritte (von Reinhardt gesammelt) als *H. saltator* bezeichnet sind. Winge hat nämlich gefunden, dass Lund's Originalexemplar des *H. laticeps* nicht mit Burmeister's Art desselben Namens[2]) identisch ist; für die mit dem Lund'schen Original übereinstimmende Form schlägt Winge desshalb den Namen *H. saltator* vor, während er den Namen *H. laticeps* in dem von Burmeister gebrauchten Sinne anwendet.

Aus einer Vergleichung mit den letzterwähnten drei Schädeln ergiebt sich, dass insofern der Schädel in Betracht kommt, die von v. Jhering gesammelten Exemplare ebenso wie ''*H. darwinii?*'' Hensel eine vermittelnde Stellung zwischen *H. laticeps* und *H. saltator* einnehmen.

1) Bei *H. laticeps* ist die Supraorbitalleiste, wie Winge hervorhebt, stark hervorragend; bei meinen Exemplaren ist sie bei etwa gleichalten Individuen schwächer und bei *H. saltator* fehlt sie gänzlich.

2) Bei *H. laticeps* ist die Länge der oberen Backenzahnreihe geringer als diejenige der des Foramen incisivum; bei den vorliegenden Exemplaren sind obere Backenzahnreihe und For. inc. etwa gleich oder ist die erstere wenig länger, während bei *H. saltator* die obere Backenzahnreihe viel länger als das Foramen incisvum ist.

3) Das hintere Ende der Nasenbeine endigt spitzig bei *H. laticeps*, stumpf bei *H. saltator*; bei den vorliegenden Exemplaren sind beide Formen vertreten.

Da ich, wie erwähnt, nur 3 Schädel von *H. laticeps* und *saltator* habe untersuchen können und ausserdem den Balg dieser Thiere nicht kenne, so wage ich aus den angeführten Thatsachen allerdings nicht den Schluss zu ziehen, dass diese Formen nicht specifisch verschieden sind. Ebensowenig halte ich mich für berechtigt, auf Grund der v. Jhering'schen Exemplare eine neue Art aufzustellen. Da die vorliegenden Schädel jedenfalls dem *H. laticeps* näher stehen als dem *H. saltator* — wenn auch von beiden etwas in Totalhabitus abweichend — führe ich dieselben als *H. laticeps* Burm. *var. intermedia* auf, ohne darauf Anspruch zu machen, denselben ihren definitiven Platz angewiesen zu haben.

Die Basilarlänge des grössten Schädels beträgt 27 mm.

Die Gestaltung des Schädels im Uebrigen ist aus den mitgetheilten Abbildungen ersichtlich.

Länge des Kopfes und Rumpfes 131 mm.
" " Schwanzes 145 "

Ohren gross, erreichen angedrückt das Ohr. Oberlippe nicht gespalten. Daumen mit Kuppennagel. Schwanz schwach behaart, am Ende ohne Haarpinsel. An der Dorsalfläche sind die Haare an der Basis grau, an der Spitze rostroth, an der Ventralfläche an der Basis ebenso, an der Spitze schmutzig weiss.

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[1]) Lund: Blik paa Brasiliens Dyreverden; Tillæg til Afhandl. 1 und 2 p. 7.

[2]) Burmeister: Systematische Uebersicht der Thiere Brasiliens; Th. I Säugethiere p. 171.

APPENDIX S

Winge's (1887: 51) Description of *Calomys coronatus* in the Original Danish

25. *Calomys coronatus* n. sp. (Pl. III, fig. 9).

Kjendes kun af den forreste Del af en Hovedskal fra Lapa da Serra das Abelhas.

Dens nærmeste Slægtning er *C. laticeps*, fra hvem den afviger i folgende:

Hovedskal. Næsehulen er bagest temmelig stærkt opsvulmet, især til Siderne; Opsvulmningen ses paa Panden som to lave Pukler og viser sig ogsaa i Overkjæbebenets Brede foran Kindtænderne. Stærk *Prc. supraorbitalis* som en afrundet Liste langs Øjehuleranden, omtrent som hos *Mus decumanus*, ikke pladeformet. Ganen bagtil uden Grube.

Maal af den afbildede Hovedskal, ad.:

Øvre Kindtænders Række	5½.
Øvre Fortænders samlede Brede	1¾.
Fra øvre *m* 1 til Fortand	9.
Ganens Brede mellem begge *m* 2	3.
Længden af *Foramen incisivum*	6⅓.
Højden af Ydervæggen af *Canalis infraorbitalis*	6.
Næsebenets Længde	ca. 14.
Pandens Brede mellem Øjehulerne	5¼.

APPENDIX T

Lund's (1840 preprint of 1841 text: 279) Description of *Mus vulpinus* in the Original Danish

Mus vulpinus, 12″6‴ lang, hvoraf Legemet 5″ 4‴, Halen 7″1‴, udmærker sig ved sin langhaarede Pels, hvis Farve oven er levende ruströd, unden hvid med et rustguult Anströg.

APPENDIX U

Wagner's (1843: 534) Description of *Hesperomys subflavus* in a Transliteration of the Original German

24. H. subflavus Wagn. Die hellfalbe Scharrmaus.

H. Ratto paululum minor, bruneo-flavus, subtus albidus, pedibus sordide albidis; cauda longitudine corporis, squamata, raripilosa.

Das äußere Ansehen ist ganz rattenähnlich, ebenso der Schwanz, der sehr fein geschuppt und mit einzelnen Härchen besetzt ist. Die Ohren sind mittelmäßig, auf der äußern und innern Seite mit feinen Härchen bewachsen, zumal am Hinterrande der letzteren. Das Gebiß ist von typischer Form. Die Füße sind schmächtig. Die Farbe der Oberseite ist bräunlichgelb, längs des Rückens und Oberkopfes schwarz gespritzelt; die Unterseite ist weißlich. Alle Haare der Oberseite sind in ihrer untern Hälfte schieferfarben, in der obern lehmgelb, längs des Rückgraths mit vielen eingemengten schwarzen Haaren. Auch auf der Unterseite sind die Haare gegen den Grund schieferfarben. An den Schnautzenseiten herrscht eine graue Farbe vor. Die Schnurren sind schwarz, einige mit weißlichen Spitzen. Der längere Haarbesatz am hintern Rande der Innenseite des Ohrs ist rostgelb. Die Füße sind weißlich behaart, was an den hintern mehr ins Schmutzige fällt; die Sohlen sind nackt. Der Schwanz ist ein ächter Rattenschwanz.

Körper	6″	0‴	Ohren	0″	8‴
Schwanz	6	0	Hinterfuß	1	1½

Die Heimath ist, nach des Naturalienhändlers Brandts Angabe, Brasilien.

APPENDIX V

Original French Translation of Azara's (1801: 86–90) Description of ''Rat Troisième, ou Rat Angouya''

C'est lé nom qui, chez les Guaranis, comprend tous les Rats, les Souris et les animaux qui leur ressemblent en quelque chose; par exemple, comme mes derniers Micourés. Cependant je le donne au Rat actuel, parce que, dans les classes d'animaux, aussi nombreuses que celles du Rat, il est impossible d'assigner à chaque espèce un nom qui la caractérise. On est donc forcé de hazarder quelques dénominations peu expressives. Indépendamment de l'impossibilité d'imposer des noms caractéristiques aux Rats, il y en a une autre qui n'est pas moindre, c'est celle de discerner les signes qui distinguent une espèce des autres; parce que quelquefois ces espèces varient, quoique les proportions soient presque les mêmes dans les mesures principales, comme il arrive par rapport à l'espèce précédente et à celle-ci; et lorsque des espèces sont plus grandes que d'autres, il reste encore du doute, puisque cette différence peut être l'effet de l'âge.

Les formes se trouvent aussi, dans certaines circonstances, si ressemblantes, qu'on ne peut les distinguer qu'avec une extrême difficulté, et encore devient-il impossible d'y parvenir, lorsqu'on ne peut avoir que peu d'individus, et à de si grands intervalles de tems, que les idées, par lesquelles l'observateur avoit cru pouvoir lier ce que son coup-d'œil lui avoit fait saisir, se sont évanouies.

Quant aux caractères que fournissent ensuite les mœurs, il se rencontre également beaucoup de ressemblances et d'identités dans les espèces de la même classe, indépendamment de ce que, pour connoître ces mœurs, il faut des siècles, et qu'il leur arrive de varier avec le climat et des circonstances particulières. Toutes ces difficultés, je les ai rencontrées et elles ne me permettent pas d'assurer, avec une certitude absolue, que le Rat actuel ou troisième, soit différent du deuxième, et je me borne à dire qu'ils me paroissent différens, en m'appuyant, non-seulement sur mon coup-d'œil et sur les différences que trouvera comme mo i celui qui comparera les deux descriptions, mais encore sur ce que le précédent m'a paru adulte, quoique plus petit; et sur ce qu'il habite la peuplade de Saint-Ignace, et que le Rat actuel a été pris à la distance de 50 lieues de là, sur le penchant d'une gorge de montagne inculte de la peuplade d'Atira, avec un autre individu de son espèce, mais plus petit.

Longueur, 11 pouces et demi (31 centimètres).

Queue de 6 pouces (16 centimètres), et que l'on peut dire pelée, quoiqu'elle ait un poil court comme le commun des Rats; sa circonférence à sa racine est de 9 lignes (2 centimètres).

Hauteur antérieure, 2 pouces 1 quart (6 centimètres); postérieure, 3 pouces et demi (9 centimètres 1 tiers).

Le front est peu moutonné, et depuis la base de l'oreille jusqu'à la pointe du museau, il y a 14 lignes (3 centimètres). L'œil est un peu plus près de l'oreille, et placé à 6 lignes (un centimètre 1 tiers) de l'autre œil. Le museau est un peu aigu et non-pelé.

Les moustaches sont nombreuses; celles de dessus sont noires, les autres blanches, et les plus grandes excèdent un peu la pointe de l'oreille, qui est à 11 lignes (2 centimètres et demi) de la pointe de l'autre oreille.

Elle est longue de 9 lignes (2 centimètres); large de 5 lignes (11 millimètres), ronde, et elle a en-dedans un poil court, principalement à la bordure postérieure, qui est sensiblement plus large que l'antérieure.

L'œil est un peu saillant; les dents sont d'une couleur orangée, et la mâchoire inférieure est un peu arquée en saillie.

Dans le pied de devant, il y a quatre doigts. L'externe naît un peu plus en arrière que l'interne, et est plus court d'une ligne (2 millimètres). Les deux du milieu naissent un peu plus en avant, et sont d'une demi-ligne (un millimètre) plus long que l'interne, et ont de petits ongles très-courbes. En outre, il y a un pouce qui naît un peu plus en arrière que tous les doigts, mais il est si court, que ce n'est qu'avec beaucoup de soin qu'on aperçoit son ongle.

Le pied de derrière a cinq doigts: l'externe et l'interne naissent parallèlement entre eux, mais l'interne est plus long et plus gros. Les autres naissent parallèlement au point où finit l'interne, et ils sont égaux entre eux. Le tarse est long de 14 lignes (3 centimètres), y compris l'ongle, velu et olivâtre, comme la plante du pied de devant.

Les deux individus étoient femelles, et leur vulve ressembloit à celle de la femelle du Rat épineux; mais il m'a paru que la plus grande n'avoit pas fait de petits.

Du museau à la queue, et sur les côtès du corps, tout est brun-cannelle, parce que les poils ont une petite pointe cannelle; puis, ils sont obscurs et enfin blancs vers la peau. Toute la partie inférieure de l'animal est blanchâtre, plus claire sous la tête, et plus foncée entre les jambes de devant; le pelage est doux, trèsserré, et le poil, qui est à la racine de l'oreille, cache le conduit de celle-ci.

APPENDIX W

Wagner's (1848: 306–307) Account of ''*Hesperomys leucogaster* Natt.'' in the Original German

1. *Hesperomys leucogaster* Natt. Die lichtbäuchige Scharrmaus.

H. supra fulvus, nigro-adspersus, subtus cano-lutescens; auriculis majusculis, pedibus fulvescentibus, cauda corpore longiore nuda.

Hesperomys leucogaster. A. Wagn. im Arch. f. Naturgesch. 1845. S. 147.

Diese Scharrmaus ist dem *Hesperomys subflavus* ähnlich, ist aber grösser, der Schwanz weit länger, die Färbung lebhafter roth und die Füsse sind bräunlich. Die Ohren sind gross, oval, breit und in ähnlicher Weise wie bei *Hesperomys Anguya* behaart; der Vorderdaumen ist sehr klein und trägt einen abgestutzen Nagel; der Schwanz ist weit länger als der Körper, nackt, geschuppt, und nur mit einzelnen Härchen zwischen den Schuppen versehen. Die Oberseite ist wie bei *Hesperomys Anguya* gefärbt, doch mit etwas mehr Roth. Die Unterseite ist schmutzig graugelblich, wobei die Haare gegen den Grund grau, nach aussen gelblich sind; die des Halses, Unterkiefers, und der Aftergegend sind einfarbig und zugleich lichter. Die Farbe auf dem Kopf ist blasser als auf dem Rücken, und gegen die Oberlippe graulich. Die Schnurren sind schwarz, die Füsse mit bräunlichen Haaren besetzt, die Sohlen sind nackt und hellfarbig. Der Schwanz ist bräunlichgrau mit einzelnen bräunlichen Haaren.

Körper	6″	10‴	Ohren	0″	10‴
Schwanz	7	9	Hinterfuss	1	6

Im Walde von *Ypanema* [San Paulo] durch *Natterer* aufgefunden. An einem Weibchen zählte er 8 Zitzen: 2 zwischen den Vorderbeinen, 2 hinter denselben, 2 vor der Hinterschenkeln, 2 hinter denselben.

APPENDIX X

Burmeister's (1854: 170–171) Account of *Hesperomys leucogaster* Natterer, Reproduced as Transliteration of the Original German

6. Hesperomys leucogaster *Natt.*
Wagner, Abhand. d. Münch. Acad. phys. Cl. V. 306. 1.

Oben röthlich gelbbraun, mit schwarzbraunen Haaren gemischt; unten grauweiß, Bauch gelblich; Schwanz länger als der Körper, fast nackt; letzterer 6⅔″, Schwanz 7¾″.

Pelz ziemlich reichlich, lang und sehr weich anzufühlen, auf der ganzen Oberseite von röthlich gelbbrauner Farbe, die Stirn, Augengegend und der Hinterrücken reiner braun, die Schnauze stark mit greis gemischt, der Nacken und die Seiten mehr rothgelb, die Backen und die Gegend am Ohr ins Grauliche spielend. Unten vom Kinn bis zum After grauweiß, die Kehle am reinsten weiß, der Bauch gelblich angeflogen. Alle Haare in der Tiefe schiefergrau, die Mitte braun, die Spitze der meisten rothbraun, sehr vieler hellgoldgelb, einiger schwarzbraun; letztere etwas längere, stärkere Grannen. Oberlippe mit weißlichem Fleck am Mundwinkel, die Seiten neben der Kehle und die Brust zwischen den Vorderbeinen graulich. An den Vorderbeinen erstreckt sich die Rückenfarbe außen bis zum Handrücken hinab, wird aber allmälig trüber; an den Hinterbeinen läßt sie die vordere Fläche neben dem Knie weiß und spielt überhaupt mehr ins Graue; der Fußrücken ist bräunlich, die Zehen sind, wie die vorderen, weiß; die nackte Sohle ist dunkel fleischfarben, bräunlich. Der lange dünne Schwanz hat sehr feine Schuppen und ein ganz kurzes, sparsames bräunliches Haarkleid, das an der Spitze einen schwachen Schopf bildet. Die langen Schnurren sind braun, die untern weiß, die Spitze der längsten reicht über die Schulter hinaus und spielt weißlich. Das Ohr ist oval, nicht eben breit, fein mit kurzen braunen Haaren besetzt, die am Vorderrande dichter stehen und länger sind. —
Ganze Länge 14″, der Kopf mit dem Rumpf 6¼–6½″, bis zum Ohr 1¼″, der Schwanz 7½–7¾″, die Hinterpfote 1⅓″, das Ohr innen 7‴. — Von St. Jao del Rey. —

Anm. 1. Die von Wagner beschriebenen Exemplare fing Natterer bei Ypanema in St. Paulo; Brants gedenkt ihrer bei Mus Aguya (Muiz. 142.), unter welchem Namen ich diese Art aus der Berliner Sammlung zur Ansicht erhielt.

2. Holochilus leucogaster *Brandt*, 1. 1. 428 2. th. 12, hat fast genau dieselben Körperverhältnisse auch ganz dieselbe Zeichnung, erscheint aber in der Abbildung, welche nach dem Leben gemacht wurde, viel heller rothgelb; fast so hell wie

H. physodes. In der Beschreibung werden die langen, bis zur Körpermitte reichenden Schnurren hervorgehoben. Die Hinterpfote soll 1″ 7‴ lang und ihre Sohle schwarz sein.

3. Eine andere ähnliche Art mit ebenso langen Schnurren unterscheidet Dr. Lund als M. mystacalis Blik p. Bras. Dyrev. III. Till. 279. Das Thier ist 12″ lang, wovon 5″ auf den Rumpf, 7″ auf den Schwanz kommen; die Farbe ist oben röthlichgrau, unten weißlich; der Schwanz endet mit einem Busch langer Haare. Sie muß den beiden vorigen Arten sehr nahe stehen.

4. Auch der Mus vulpinus desselben Schriftstellers (a.a.O.) dürste hierher gehören, wenigstens in die Nähe dieser einander sehr ähnlichen Arten kommen, wenn nicht gar wie ich vermuthe, mit H. leucogaster zusammenfallen. Seine Länge ist 12″ 6‴, wovon 5″ 5‴ dem Rumpf, 7″ 1‴ dem Schwanz zustehen; der Pelz ist ungemein langhaarig, oben lebhaft rostroth, unten weiß mit rostgelben Anflug. —

APPENDIX Y

Hensel's (1872: 36–37) Description of *Hesperomys ratticeps* in the Original German

22) *Hesperomys ratticeps* n. sp. Fig. 15 u. 25

Im Oberkiefer hat m1 den Gipfel des Pfeilers am vorderen Ende durch einen flachen, medianen Einschnitt in zwei Spitzen getheilt, die weniger deutlich sind als die Höcker der Zahnkronen. Bei m3 ist bloß das vordere Höckerpaar deutlich entwickelt, der hintere Schmelzwinkel ist verkümmert, seine Höcker sind kaum angedeutet. Schneidezähne an der Schneide zusammen 2,40 Mm. breit.

Im Unterkiefer ist bei m1 der vordere Pfeiler deutlicher in zwei Spitzen getheilt und die Furche ist selbst auf der Vorderseite des Zahnes zu bemerken, bei m3 ist das hintere Höckerpaar verkümmert und in einen stumpfkegelförmigen Pfeiler mit einer Vertiefung auf dem Gipfel verschmolzen. Bei m2 und m3 wird vor dem Aufsenhöcker des vorderen Höckerpaares durch einen basalen Wulst eine schmale Furche gebildet, die das Querthal repräsentirt, durch welches in m1 der vordere Pfeiler von dem folgenden Höckenpaare getrennt wird.

Obere Backenzahnreihe 6,0 Mm. — m1 2,60 — m2 1,80 — m3 1,50 Mm. lang. Untere Backenzahnreihe 6,0 Mm. — m1 2,45 — m2 1,90 — m3 1,85 Mm. lang.

Die Nasenbeine reichen so weit wie die Proc. front. der Oberkiefer. Die Breite der Stirn zwischen den Augen etwas kleiner als die Länge der oberen Backzahnreihe. Das Interparietale groß, wie bei Mus decumanus. Der Supraorbitalrand ohne scharfe Kante, aber auch nicht abgerundet. Foramina incis. dicht hinter der Mitte am breitesten, enden unmittelbar vor der Querlinie der ersten Zähne etwas spitz, aber stumpfer als vorn.

Bas. lg. des größten Schädels (altes ♀) 31,0 Mm. Nasenbeine 14,4 Mm. Foram. incis. 8,0 Mm. Breite der Stirn zwischen den Augen 5,0 Mm. Sagittaler Durchmesser des Interparietale 3,9 Mm. Frontaler Durchmesser desselben 10,6 Mm.

An eniem Skelet 12 Rippenpaare, 7 rippenlose Lendenwirbel, 3 Sacralwirbel, der dritte ohne alle Verbindung mit dem Becken. 39 Schwanzwirbel, der 17te Wirbel der diaphragmatische.

Die Ohren sind groß, bei frischen Exemplaren reichen sie bis an den vorderen Augenwinkel, bei den in Spiritus erhärteten Examplaren nicht bis an das Auge. Oberlippe gespalten. Am Daumen der Hand ein Stumpfer Kuppennagel. Die Sohle des Tarsus kahl. Das Tuberkel an der Innenseite der Sohle lang und stark. Der lange Schwanz sehr fein und schwach behaart, am Ende mit einem schwachen Haarpinsel, fein aber deutlich beschuppt.

Die Farbe ist ähnlich der des Mus decumanus. Die ganze Oberseite gelblich grau. Die Grundwolle in der Tiefe mäusegrau, an der Spitze gelb (rehfarben), die Grannen schwarz. Auf der ganzen Unterseite ist die Grundwolle gelblich weiß, an der Kehle fast weiß. Die Ohren auf der Außenseite nach dem Rande zu mit feinen Härchen bedeckt. Der schwanz einfarbig.

An dem größten Exemplar in Spiritus messen Kopf und Rumpf 155 Mm., Schwanz 210 Mm., Tarsus 34 Mm.

Das Thier wurde nur im Urwalde gefunden, wo es zuweilen auf Bäumen angetroffen wird, aber auch die Vorrathshütten in den Plantagen besucht.

Gesammelt wurden 2 Skelete, 1 Schädel, 6 große Exemplare und ein Foetus in Spiritus.

APPENDIX Z

Winge's (1887: 50) Description of *Calomys rex* in the Original Danish

24. **Calomys rex** n. sp. (Pl. III, fig. 8).

Kun jordfunden, men temmelig almindelig, i Hulerne Lapa do Capão Secco, da Escrivania Nr. 3, Nr. 5 og Nr. 11, en Salpeterhule ved Escrivania, Lapa da Quebra Chavelha og da Serra das Abelhas.

Kjendes kun af den forreste Del af Hovedskallen.

Det er en temmelig enestaaende Art; i Pandens Form minder den noget om *C. anoblepas*. Den er større end de andre *Calomys*-Arter, omtrent som *Nectomys squamipes*.

Fra *C. laticeps* afviger den i følgende:

Den er meget større.

Hovedskal. Temmelig skarp Kam efter Læbemuskel paa Overkjæbebenets Krop foran Kindtænderne. Panden smal, sammentrykt, nedhulet paalangs. Ingen *Prc. supraorbitalis*; Pandens Øjehulerand temmelig skarp. Benganen synes at stæekke sig særlig langt tilbage.

Maal af den afbildede Hovedskal (1.), ad., fra Lapa da Escrivania Nr. 5 (Underkjæben fra Lapa da Serra das Abelhas) og andre:

Øvre Kindtænders Række	6½.	Længden af *Foramen incisivum*	9¼.
Nedre Kindtænders Række	6⅓.	Højden af Ydervæggen af *Canalis infraorbitalis*	8.
Øvre Fortænders samlede Brede	2¾.	Næsebenets Længde	17.
Fra øvre *m* 1 til Fortand	11½.	Pandens Brede mellem Øjehurlene	5⅓.
Fra nedre *m* l til Fortand	5.	Underkjæbens Længde	22½.
Ganens Brede mellem begge *m* 2	3½.	Underkjæbens Hjde under *m* 1	6¼.

	Capão Secco.		Escrivania 5.			S. d. Abelh.	
	2. vet.	3. juv.	4. ad.	5. vet.	6. ad.	7. vet.	8. juv.
Øvre Kindtænders Række	6 ⅓	6 ½	6 ⅔	6 ½	6 ½	6 ¾	7.
Fra øvre *m* til Fortand	12		11	11 ¼		11 ⅔	9 ¾.
Længden af *For. incisivum*	9 ⅓		9	9⅔		9 ⅓	8.
Næsebenets Længde						17 ½	

	Capão Secco.	Escr. 3.		Escr. 5.		Serra das Abelhas				
	9. ad.	10. vet.	11. ad.	12. ad.	13. ad.	14. ad.	15. ad.	16. ad.	17. ad.	18. ad.
Nedre Kindtænders Række	6 ½	6 ⅓	6 ½	7	6 ⅔	6 ¼	6 ¼	6 ⅓	7 ⅓	6