TAMARA ALMEIDA FLORES

DIVERSIDADE MORFOLÓGICA E MOLECULAR DO GÊNERO *Oecomys* THOMAS, 1906 (RODENTIA: CRICETIDAE) NA AMAZÔNIA ORIENTAL BRASILEIRA

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MUSEU PARAENSE EMÍLIO GOELDI
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CURSO DE MESTRADO EM ZOOLOGIA

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Dissertação apresentada ao Programa de Pós-Graduação em Zoologia, Curso de Mestrado, da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do grau de mestre em Zoologia.

Orientador: Dr. Rogério Vieira Rossi
Co-orientador: Dr. José de Sousa e Silva Júnior

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EPÍGRAFE

“A variação é essencial para o processo evolutivo.”
(Mark Ridley)

DEDICATÓRIA

A todos aqueles que trabalham com pequenos mamíferos, e ao Arlindo Júnior (*in memoriam*).

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SUMÁRIO

RESUMO

Os roedores arborícolas do gênero *Oecomys* possuem distribuição reconhecida para áreas de floresta tropical e subtropical da América Central e do Sul, e compreendem 17 espécies atualmente reconhecidas, além de duas descritas, mas não nomeadas, reconhecidas em estudos prévios. Destas, apenas seis têm ocorrência esperada para a Amazônia oriental brasileira. A delimitação das espécies com base apenas em caracteres morfológicos é complicada, de forma que diversos táxons nominais já foram associados ao gênero e diversos arranjos taxonômicos foram propostos. Na única revisão taxonômica para o gênero, realizada há 50 anos, foram reconhecidas apenas duas espécies politípicas. Desde então, vários trabalhos envolvendo análises morfológicas, moleculares e cariotípicas têm demonstrado que há uma maior diversidade de espécies em *Oecomys*, resultando em descrições de espécies novas e revalidações de espécies anteriormente sinonimizadas. Este trabalho buscou caracterizar a variação morfológica e a diversidade molecular das espécies com ocorrência na Amazônia oriental brasileira. Para isto, empregamos análises filogenéticas com base no gene mitocondrial citocromo-*b* a fim de definir clados que representassem espécies, para as quais descrevemos a morfologia externa e craniana. Como resultado, reconhecemos 11 espécies com ocorrência para o leste da Amazônia brasileira, das quais cinco são esperadas para a região (*Oecomys auyantepui*, *O. bicolor*, *O. paricola*, *O. rex* e *O. rutilus*), duas são registradas pela primeira vez para o bioma Amazônia (*Oecomys catherinae* e *O. cleberi*) e quatro espécies são novas ou não reconhecidas como válidas atualmente, aqui denominadas *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C e *Oecomys* sp. D. Além disso, corroboramos estudos moleculares prévios em que *Oecomys bicolor* é um complexo de espécies, com base na alta taxa de divergência nucleotídica apresentada (7,5 %). Observamos dimorfismo sexual e variação ontogenética na morfometria craniana da espécie *Oecomys paricola*, e para efeito de comparação extrapolamos estas variações para as demais espécies tratadas aqui. Sugerimos também uma hipótese filogenética entre as espécies do gênero a partir de 653 pb do gene citocromo-*b*, sendo esta a filogenia mais abrangente para *Oecomys* publicada até o momento, devido ao elevado número de espécies incluídas (11 das 16 espécies atualmente reconhecidas e sete prováveis novas espécies) e a amplitude geográfica das amostras aqui utilizadas.

ABSTRACT

The arboreal rice rats, genus *Oecomys*, are distributed in tropical and subtropical areas from Central and South America, with 17 currently recognized species and another two species already described in earlier studies but still unnamed. Six of these species are expected to occur in eastern Brazilian Amazon. Because defining the species limits inside *Oecomys* based only on morphological characters is a complicated task, many nominal taxa have already been associated to the genus, and different taxonomic arrangements have been proposed by specialists. Despite of this taxonomic instability, there is only one taxonomic review for the genus carried out 50 years ago, in which only two polytypical species were recognized. However, several recent studies based on morphological, molecular and karyotypical data have been showing that the species diversity inside *Oecomys* is largely underestimated, resulting in recent descriptions of new taxa or revalidation of previously synonymized species. This work aimed to assess the species diversity inside this genus in the eastern Brazilian Amazon by investigating the molecular and morphological variation in regional specimens. We employed phylogenetic analysis based on cytochrome-*b* in order to define clades that may represent species, and described the external and cranial morphology of these recognized species. As a result, we recognized 11 species in the eastern Amazonian forest in Brazil, of which five are already expected to occur in this area (*Oecomys auyantepui*, *O. bicolor*, *O. paricola*, *O. rex*, and *O. rutilus*), two are recorded for the first time in the biome Amazonia (*Oecomys catherinae* and *O. cleberi*), and the four are either new or not currently recognized species (i.e. synonyms), herein referred as *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C, and *Oecomys* sp. D. Moreover, we suggest that *Oecomys bicolor* is a species complex, based in the high nucleotide divergence we found (7.5 %), corroborating previous molecular studies. We observed sexual dimorphism and ontogenetic variation on cranial morphometry in the species *Oecomys paricola*, and for comparison purposes we treated all other species herein studied as exhibiting this kind of dimorphism. We also suggest a phylogenetic hypothesis among the species of this genus based on 653 bp of cytochrome-*b*. This is the most comprehensive phylogeny for *Oecomys* published to date, due to the great number of species included in the analysis (11 of the 16 currently recognized species plus seven probably new species), and the wide-ranging geographic area included in our sample.

INTRODUÇÃO GERAL

A superfamília Muroidea Miller e Gidley, 1918 é um táxon monofilético de roedores composto por seis famílias: Calomyscidae, Cricetidae, Muridae, Nesomyidae, Platacanthomyidae e Spalacidae (MUSSER e CARLETON, 2005). Esta superfamília é caracterizada por ausência de pré-molares, tamanho decrescente dos molares (o primeiro molar maior que o segundo e este maior que o terceiro), presença de forâmen infra-orbital amplo, frontais comumente estreitos, bulas pouco desenvolvidas e jugais curtos (MOOJEN, 1952; CARLETON e MUSSER, 1984). Sua monofilia é fortemente apoiada por estudos paleontológicos, morfológicos e moleculares (CARLETON e MUSSER, 1984; MUSSER e CARLETON, 2005).

A família Cricetidae reúne os roedores que possuem um arranjo bisserial das cúspides molares, com retenção de uma conexão longitudinal (muro/murídeo) entre elas e a formação de um anterocone/anteroconídeo nos primeiros molares (Figura 1; MUSSER e CARLETON, 2005). Os cricetídeos estão distribuídos em seis subfamílias: Arvicolinae, Cricetinae, Lophiomyinae, Neotominae, Sigmodontinae e Tylomyinae. A subfamília Sigmodontinae, que contém a grande maioria das espécies de roedores sul-americanos, tem distribuição geográfica restrita às Américas e abriga atualmente 386 espécies em 81 gêneros e nove tribos, a saber: Abrotrichini, Akodontini, Ichthyomyini, Oryzomyini, Phyllotini, Reithrodontini, Sigmodontini, Thomasomyini e Wiedomyini (REIG, 1980, 1984; SMITH e PATTON, 1999; MUSSER e CARLETON, 2005; WEKSLER *et al.*, 2006; D'ELÍA *et al.*, 2007).

Figura 1 – Série molar superior (esquerda) e inferior (direita) de *Oecomys auyantepui* (IEPA2444), ressaltando a presença de anterocone/anteroconídeo nos primeiros molares e a conexão longitudinal (muro/murídeo) entras as cúspides molares. Foto: Tamara Flores, 2010.

O gênero *Oecomys* e outros 27 gêneros estão agrupados na tribo Oryzomyini (WEKSLER *et al.*, 2006). De acordo com Musser e Carleton (2005), este gênero conta com quinze espécies atualmente reconhecidas como válidas: *Oecomys auyantepui* Tate, 1939, *O. bicolor* (Thomas, 1860), *O. catherinae* Thomas, 1909, *O. cleberi* Locks, 1981, *O. concolor* (Wagner, 1845), *O. flavicans* (Thomas, 1894), *O. mamorae* (Thomas, 1906), *O. paricola* (Thomas, 1904), *O. phaeotis* (Thomas, 1910), *O. rex* Thomas, 1910, *O. roberti* (Thomas, 1904), *O. rutilus* Anthony, 1921, *O. speciosus* (J.A. Allen e Chapman, 1893), *O. superans* Thomas, 1911 e *O. trinitatis* (J.A. Allen e Chapman, 1893), distribuídas em áreas de floresta tropical e subtropical das Américas Central e do Sul, incluindo Costa Rica, Trinidad, Panamá, Venezuela, Colômbia, Equador, Peru, Bolívia, Guiana, Guiana Francesa, Suriname e Brasil (HERSHKOVITZ, 1960). Além destas, uma nova espécie (*O. sydandersoni*) com distribuição restrita ao nordeste da Bolívia foi recentemente descrita por Carleton *et al.* (2009).

Os representantes deste gênero (Figura 2) possuem comprimento da cabeça e corpo entre 71 e 176 mm, e comprimento da cauda entre 80 e 192 mm. A pelagem do dorso varia de castanho-escuro a castanho-alaranjado, as laterais são mais claras que o dorso e possuem limite bem definido em relação ao ventre. A pelagem do ventre pode ser completamente de cor branca, creme com pêlos de base cinza, ou com este segundo padrão e manchas completamente de cor branca ou creme na linha mediana do ventre. A pelagem da cabeça é geralmente similar à do corpo. Possuem vibrissas longas, que ultrapassam o limite posterior das orelhas quando posicionadas rente ao corpo; patas relativamente curtas, largas e de cor clara, com uma mancha ligeiramente escura na superfície dorsal; e almofadas plantares bem desenvolvidas. A cauda apresenta porção terminal pilosa, podendo ou não formar um pincel caudal. Possuem quatro pares de mamas: peitoral, pós-axial, abdominal e inguinal (BONVINCINO *et al.*, 2008).

As espécies de *Oecomys* são arborícolas e habitam as áreas florestais da Floresta Amazônica e Mata Atlântica, além de matas de galeria e outras formações florestais do Cerrado e Pantanal. Fazem ninhos em buracos de árvores, emaranhado de epífitas ou trepadeiras, copas de palmeiras ou ninhos de pássaros abandonados. Estes roedores são de hábito noturno, vivem em pares, famílias ou colônias, e normalmente forrageiam nas árvores, mas podem ir até o chão em busca de água e alimento (HERSHKOVITZ, 1960; OLIVEIRA e BONVINCINO, 2006; BONVINCINO *et al.*, 2008).

Figura 2 – *Oecomys* sp. B. Foto: Tamara Flores, 2008.

Para o leste da Amazônia brasileira é esperado que ocorram seis espécies de *Oecomys* assim distribuídas: *Oecomys auyantepui*, presente na Venezuela, Guianas e Brasil, no estado do Amapá; *O. bicolor*, presente do Panamá à Colômbia, Equador, Peru, Bolívia, Venezuela, Guianas e no Brasil, nos estados do Amapá, Roraima, Amazonas, Pará, Acre, Rondônia, Mato Grosso, Mato Grosso do Sul, Tocantins, Goiás, Bahia, Minas Gerais e no Distrito Federal; *O. paricola*, registrado apenas para o estado do Pará, nas proximidades de Belém; *O. rex*, presente no norte dos estados do Amapá e Amazonas; *O. rutilus*, presente na Venezuela, Guianas e no Brasil, no estado do Amazonas; e *O. trinitatis*, estendendo-se da Costa Rica até o Brasil, incluindo Guianas, Trinidad e Tobago, Colômbia até o Peru, e no Brasil os estados do Acre, Amazonas, Roraima e Pará (MOOJEN, 1952; PATTON *et al*., 2000; VOSS *et al*., 2001; COSTA, 2003; MUSSER e CARLETON, 2005; OLIVEIRA e BONVINCINO, 2006; BONVINCINO *et al.*, 2008).

História taxonômica do gênero *Oecomys*

O primeiro nome proposto para um roedor do gênero *Oecomys* foi *Mus cinnamomeus* Pictet e Pictet, 1844, com base em um exemplar proveniente do leste do Brasil. No entanto, este nome não foi considerado válido, pois estava pré-ocupado por uma espécie de outro roedor, *Mus cinnamomeus* Lichtenstein, 1830, associado a um *Proechimys*. Desta forma, o nome mais antigo disponível para estes orizomíneos era *Hesperomys concolor* Wagner, 1845, táxon descrito através de um exemplar coletado no alto Rio Negro, noroeste do Brasil.

Após uma revisão do gênero *Thomasomys* realizada por Bangs (1900), na qual diferenciou este gênero de *Oryzomys* com base no número de mamas (seis em *Thomasomys* e oito em *Oryzomys*) e no formato do palato, sendo curto (fossa mesopterigóide entendendo-se anteriormente além do alvéolo de M3) e sem perfurações em *Thomasomys*, enquanto que em *Oryzomys* o palato é longo (fossa mesopterigóide não se estende anteriormente além da região posterior do osso maxilar) e com perfurações laterais, Thomas (1906) determinou os caracteres para a definição do gênero *Rhipidomys*, mantendo neste gênero as espécies que possuíam seis mamas, cauda longa e com pincel caudal bem desenvolvido, e o palato com as características de *Thomasomys*, e realocando para o gênero *Oryzomys* as espécies que possuíam oito mamas e as características do palato de *Oryzomys*, sendo estas *dryas* Thomas, 1900, *phaeotis* Thomas, 1901, *benevolens* Thomas, 1901, *rosilla* Thomas, 1904 e *paricola* Thomas, 1904, e o exemplar descrito por Tomes (1860), *Hesperomys bicolor*. Entretanto, Thomas (1906) propôs o subgênero *Oecomys* associado a *Oryzomys* para alocar estas espécies que também diferenciavam-se de outros orizomíneos por apresentar o crânio relativamente grande e arredondado, como *Rhipidomys*; pés largos; quinto dedo longo; pelagem corporal cobrindo a parte basal da cauda e presença de pincel caudal. Além disso, Thomas (1906) incluiu no subgênero *Oecomys* outros táxons nominais que ele havia descrito e associado previamente a *Rhipidomys*, a saber: *marmosurus* Thomas, 1899; *mamorae* Thomas, 1906 e *roberti* Thomas, 1904. Outros táxons nominais atualmente associados a *Oecomys* e já descritos naquela ocasião, tais como *Hesperomys concolor* e outros originalmente associados a *Oryzomys* (*speciosus* J.A. Allen e Chapman, 1893; *trinitatis* J.A. Allen e Chapman, 1893; *flavicans* Thomas, 1894; *subluteus* Thomas, 1898; *fulviventer* J.A. Allen, 1899; *palmarius* J.A. Allen, 1899; *trichurus* J.A. Allen, 1899; *tectus* Thomas, 1901 e *klagesi* J.A. Allen, 1904) não foram prontamente incluídos em *Oecomys* por Thomas (1906).

O subgênero *Oecomys* foi elevado ao nível de gênero por Thomas (1909), ao acrescentar na diagnose do gênero o fato de que a borda externa da raiz anterior do zigomático não se projeta anteriormente, enquanto que em *Oryzomys* sempre há esta projeção bem marcada. No entanto, Ellerman (1941) questionou a validade deste táxon, inclusive como subgênero, alegando para isso as várias semelhanças exibidas pelas espécies listadas para *Oecomys* e *Oryzomys*.

Posteriormente ao trabalho de Thomas (1906) foram associados outros 26 táxons ao gênero *Oecomys* (Tabela 1), das quais três originalmente associadas ao gênero *Oryzomys* e as demais pertencentes ao subgênero ou gênero *Oecomys*.

Tabela 1 - Táxons nominais associados à *Oecomys* de acordo com Musser e Carleton (2005) e Carleton *et al.* (2009), e suas respectivas localidades-tipo. Os táxons atualmente reconhecidos como espécies possuem asterisco (*).

Táxon Nominal	**Localidade-tipo**
*auyantepui** Tate, 1939	Venezuela, Estado de Bolívar, leste do Río Caroni, Cordilheira de Auyán-Tepuí, 1100 m.
*bicolor** Tomes, 1860	Equador, Morona-Santiago, Gualaquiza, Río Gualaquiza, 885m.
benevolens Thomas, 1901	Bolívia, La Paz, alto Río Beni, Chimate, 700m.
dryas Thomas, 1900	Equador (noroeste), Imbabura, Río Mira, Paramba, 1100 m.
endersi Goldman, 1933	Panamá, Ilha de Barro Colorado, Zona do Canal.
florenciae J.A. Allen, 1916	Colômbia, Caquetá, alto Río Caquetá, Río Orteguaza, Florencia.
milleri J.A. Allen, 1916	Brasil, Mato Grosso, Barão de Melgaço, Rio Madeira, alto Gy-Paraná, Rio Conguiaru.
nitedulus Thomas, 1910	Guiana, Demerara, baixo Essequibo River, 13 milhas da boca.
occidentalis Hershkovitz, 1960	Equador (noroeste), Imbabura, Río Mira, Paramba, 1100 m.
phelpsi Tate, 1939	Venezuela, Estado de Bolívar, leste do Río Caroni, Cordilheira de Auyán-Tepuí, 1100 m.
rosilla Thomas, 1904	Venezuela, Estado de Bolívar, Río Orinoco, baixo Río Caura, La Unión.
trabeatus G.M. Allen e Barbour, 1923	Panamá (leste), Darién, Río Jesuíto (ou Jesusito).
*catherinae** Thomas, 1909	Brasil, Estado de Santa Catarina, Joinville.
bahiensis Hershkovitz, 1960	Brasil, Estado da Bahia, lhéus.
cinnamomeus Pictet e Pictet, 1844	Brasil, Estado da Bahia, lhéus.
*cleberi** Locks, 1981	Brasil, Distrito Federal, Universidade de Brasília, Fazenda Água Limpa.
*concolor** Wagner, 1845	Brasil, Estado do Amazonas, Rio Curicuriari, tributário do alto Rio Negro, abaixo de São Gabriel.
marmosurus Thomas, 1899	Colômbia (leste), Vichada, meio Río Orinoco, Maipures.
*flavicans** Thomas, 1894	Venezuela, Estado de Mérida, Mérida, 1600 m.
illectus Bangs, 1896 ou 1898	Colômbia, Magdalena, Sierra Nevada de Santa Marta, Pueblo Viejo, 853 m.
mincae J.A. Allen, 1913	Colômbia, Magdalena, Sierra Nevada de Santa Marta, Minca.
*mamorae** Thomas, 1906	Bolívia, Cochabamba, alto Río Mamoré, Mosetenes.
*paricola** Thomas, 1904	Brasil, Estado do Pará, Igarapé Assú, 50 m.

Continuação da Tabela 1

Táxon Nominal	**Localidade-tipo**
*phaeotis** Thomas, 1901	Peru, Puno, alto Río Inambari, Sagrario, 1000 m.
*rex** Thomas, 1910	Guiana, Demerara, Supenaam River.
regalis Hershkovitz, 1960	Guiana, Demerara, Supenaam River.
*roberti** Thomas, 1904	Brasil, Estado do Mato Grosso, Santa Anna da Chapada (=Chapada dos Guimarães), 800 m.
guianae Thomas, 1910	Guiana, Demerara, Supenaam River.
tapajinus Thomas, 1909	Brasil, Estado do Pará, Río Tapajós, Río Jamanchin, Santa Rosa.
*rutilus** Anthony, 1921	Guiana, Mazaruni-Potaro, Kartabo.
*speciosus** J.A. Allen e Chapman, 1893	Trinidad, Princes Town.
caicarae J.A. Allen, 1913	Venezuela, Estado de Bolívar, Río Orinoco, Caicara.
trichurus J.A. Allen, 1899	Colômbia, Magdalena, Sierra Nevada de Santa Marta, El Líbano, próximo a Bonda.
*superans** Thomas, 1911	Equador, Pastaza, Rio Bobonaza, Canelos, 640 m.
melleus Anthony, 1924	Equador (leste), Santiago-Zamora, Zamora, 1000 m.
palmeri Thomas, 1911	Equador, Pastaza, Rio Bobonaza, Canelos, 640 m.
*trinitatis** J.A. Allen e Chapman, 1893	Trinidad, Princes Town.
frontalis Goldman, 1912	Panamá, Corozal, Zona do Canal.
fulviventer J.A. Allen, 1899	Venezuela, Sucre, Cumanacoa, Río Manzanares, Quebrada Seca.
helvolus J.A. Allen, 1913	Colômbia, Meta, Río Meta, Villavivencio.
klagesi J.A. Allen, 1904	Venezuela, Estado de Bolívar, baixo Río Caura, El Llagual (Yagual), próximo a Maripa.
osgoodi Thomas, 1924	Peru, Amazonas, Moyobamba, 820 m.
palmarius J.A. Allen, 1899	Venezuela, Sucre, Cumanacoa, Río Manzanares, Quebrada Seca.
splendens Hayman, 1938	Trinidad (sudeste), Mayaro.
subluteus Thomas, 1898	Colômbia, Cundinamarca, oeste da Cordilheira Oriental.
tectus Thomas, 1901	Panamá, Chiriquí, Bugaba (Bugava), 250 m.
vivencianus J.A. Allen, 1913	Colômbia, Meta, Río Meta, Villavivencio.
*sydandersoni** Carleton, Emmons e Musser, 2009	Bolívia, Departamento de Santa Cruz, Província Velasco, El Refugio Huanchaca, 210 m.

A única revisão taxonômica ampla para o gênero *Oecomys* foi realizada por Hershkovitz (1960), considerando-o subgênero de *Oryzomys*. Este autor agrupou 25 espécies reconhecidas na época em apenas duas, *O. bicolor* e *O. concolor*. De acordo com ele, os espécimes de *O. concolor*, quando comparados aos de *O. bicolor*, apresentam maior tamanho, pés de menor tamanho em relação ao corpo, cauda mais longa em relação ao corpo, e crista temporal bem desenvolvida. Neste mesmo trabalho, Hershkovitz (1960) reconheceu quatro subespécies para *O. bicolor (bicolor*, *phaeotis*, *trabeatus* e *occidentalis*); e cinco subespécies para *O. concolor (concolor, superans, speciosus, roberti* e *bahiensis*).

Os autores que investigaram a diversidade taxonômica de *Oecomys* após a revisão de Hershkovitz (1960) discordaram entre si com relação à categoria supra-específica a qual este grupo deveria ser alocado. Cabrera (1960) e Hall (1981) seguiram Hershkovitz (1960), mas Gardner e Patton (1976), Carleton e Musser (1984) e Reig (1984, 1986) reconheceram *Oecomys* como gênero válido. Somente a partir do catálogo taxonômico publicado por Musser e Carleton (1993) tornou-se consenso o status genérico de *Oecomys*. Estudos recentes de filogenia que incluem algumas espécies de *Oecomys* publicados até o presente corroboram o monofiletismo do gênero (PATTON e DA SILVA, 1995; SMITH e PATTON, 1999; PATTON *et al.*, 2000; ANDRADE e BONVINCINO, 2003; WEKSLER, 2003, 2006).

Muitos autores consideraram o arranjo de espécies proposto por Hershkovitz (1960) inadequado, reconhecendo, portanto, maior número de espécies para o gênero (MUSSER e CARLETON, 1993, 2005; VOSS *et al.*, 2001; PATTON *et al.*, 2000; OLIVEIRA e BONVINCINO, 2006; BONVINCINO *et al.*, 2008). Posteriormente, Patton *et al.* (2000) registraram cinco espécies ao longo do rio Juruá, corroborando o arranjo taxonômico proposto por Musser e Carleton (1993). Entre as espécies reconhecidas por Patton *et al.* (2000) está uma espécie nova, não nomeada até o presente momento. Em seguida, Voss *et al.* (2001) reconheceram quatro espécies para a região da Guiana Francesa, incluindo a revalidação de *Oecomys auyantepui* para a região das Guianas. Recentemente, Carleton *et al.* (2009) descreveram *O. sydandersoni* para o nordeste da Bolívia.

Em suma, de acordo com Musser e Carleton (2005) e Carleton *et al.* (2009) existem 48 táxons nominais associados a *Oecomys*, dos quais 16 representam espécies atualmente reconhecidas (Tabela 1). Entre estas espécies, *Oecomys bicolor* e *O. trinitatis* são reconhecidas como possíveis complexos de espécies por estes autores.

Filogenia molecular e citogenética do gênero *Oecomys*

Trabalhos envolvendo filogenia molecular e citogenética têm sido realizados com o objetivo de compreender as relações filogenéticas e a radiação dos roedores cricetídeos da América do Sul e corroboram o monofiletismo da tribo Oryzomyini e dos gêneros que a constituem (GARDNER e PATTON, 1976; SMITH e PATTON 1991, 1993, 1999; D'ELIA, 2003; WEKSLER, 2003, 2006).

Estudos importantes sobre roedores sigmodontíneos envolvendo filogenias moleculares realizados desde 1991 utilizaram o gene mitocondrial citocromo-*b* como marcador molecular (SMITH e PATTON, 1991, 1993, 1999; PATTON *et al*., 2000; ANDRADE e BONVINCINO, 2003; D'ELIA, 2003; MIRANDA *et al.*, 2007; D'ELIA *et al*., 2008; CATZEFLIS e TILAK, 2009) e de acordo com Johns e Avise (1998) e Avise e Walker (1999) este gene apresentou clados altamente congruentes com os limites de espécies baseados em estudos taxonômicos clássicos, o que significa que o citocromo-*b* é relevante em estudos de biodiversidade (BRADLEY e BAKER, 2001).

As informações sobre as relações filogenéticas dentro do gênero *Oecomys* são parcamente conhecidas (PATTON *et al.*, 2000). Não existe uma filogenia molecular completa para o gênero, mas há estudos sobre filogenia que incluem algumas de suas espécies (Figura 3), entre os principais algumas somente com dados moleculares (PATTON e DA SILVA, 1995; SMITH e PATTON, 1999; PATTON *et al.*, 2000; ANDRADE e BONVINCINO, 2003; WEKSLER, 2003) e uma com dados moleculares e morfológicos combinados (WEKSLER, 2006). Todos corroboram o monofiletismo do gênero, e o mais abrangente deles aponta *Euryoryzomys* e *Hylaeamys* (anteriormente reconhecidos como *Oryzomys*) como grupos filogeneticamente próximos de *Oecomys* (WEKSLER, 2006).

A primeira filogenia molecular que incluiu o gênero *Oecomys* foi a proposta por Patton e Da Silva (1995; Figura 3A). Os autores utilizaram 801 pb de citocromo-*b* para buscar elucidar as relações do gênero *Scolomys* com outros orizomínios dos gêneros *Microryzomys*, *Neacomys*, *Nectomys*, *Oecomys*, *Oligoryzomys* e *Oryzomys*, empregando duas espécies de tomasomíneos como grupo externo, *Thomasomys aureus* e *Rhipidomys leucodactylus*. Foram utilizadas sequencias de *Oecomys bicolor*, *O. roberti*, *O. trinitatis*, *O. superans* e uma espécie inderteminada procedentes do Rio Juruá, Brasil. A divergência entre os gêneros *Oecomys* e *Hylaeamys* e *Euryoryzomys* encontrada foi em média 25.6 %, e a divergência intragenérica de

Oecomys foi em média 14.8 %. As relações encontradas entre as espécies do gênero tiveram um apoio de *bootstrap* muito baixo, sendo 53 % para o clado (*O. roberti*, *O. superans*) e abaixo de 50 % para os clados (*O. bicolor*, *Oecomys* sp.), e ((*O. bicolor*, *Oecomys* sp.), (*O. roberti*, *O. superans*)). O suporte do clado que incluiu todas as espécies do gênero foi de 88 %.

Smith e Patton (1999) propuseram uma filogenia sobre as relações entre os roedores sigmodontíneos da América do Sul, com base em 801 pb de citocromo-*b* (Figura 3B). Nesta filogenia foram incluídas três espécies de *Oecomys*, além de uma não identificada. Nesta filogenia, *O. trinitatis* e *O. superans* formam um grupo monofilético, entretanto a espécie *O. bicolor* é parafilética, sendo que um ramo é irmão de *O. trinitatis* + *O. superans* e outro é grupo irmão deste clado ((*O. trinitatis*, *O. superans*), *O. bicolor*). Além disso, a espécie não identificada consta como táxon mais basal. A divergência intraespecífica encontrada variou de 0.04 % a 9.7 %. Novamente o suporte encontrado para as relações interespecíficas foi muito baixo, sendo 59 % para o clado (((*O. trinitatis*, *O. superans*), *O. bicolor*), *O. bicolor*), e menos de 50 % para os demais clados. O suporte do clado de todas as espécies do gênero foi de 72 %.

Patton *et al.* (2000) realizaram uma análise filogenética incluindo apenas exemplares procedentes do Rio Juruá, com base em 801 pb do citocromo-*b*. Os valores de *bootstrap* entre as espécies sempre foi inferior a 50 %, e na árvore de consenso estrito do gênero todas as espécies aparecem em politomia. Estes autores verificaram que as distâncias moleculares estimadas entre as espécies são equivalentes entre si, variando de 7,2 % a 9,8 %. São valores baixos se comparados aos de outros gêneros politípicos da mesma região, como *Neacomys* (13,2 % de divergência média entre as espécies) e o gênero *Hylaeamys* (15 % de divergência média). Os autores sugeriram que tal achado pudesse indicar que o gênero *Oecomys* teve um ciclo de especiação mais recente do que os outros dois. Para as espécies *Oecomys bicolor* e *O. roberti*, Patton *et al.* (2000) encontraram divergência média de 5,43 % e 4,1 %, respectivamente, entre as populações.

A filogenia proposta por Andrade e Bonvincino (2003) foi baseada em 801 pb de citocromo-*b* (Figura 3C) e contou com cinco espécies, sendo uma não identificada. As autoras apresentaram duas filogenias, uma obtida através do critério de parsimônia e outra através de máxima verossimilhança. Em geral, os resultados obtidos neste estudo corroboram os

resultados de Patton *et al.* (2000), e mostram que *O. bicolor* é um táxon parafilético, indicando que pode se tratar de um complexo de espécies.

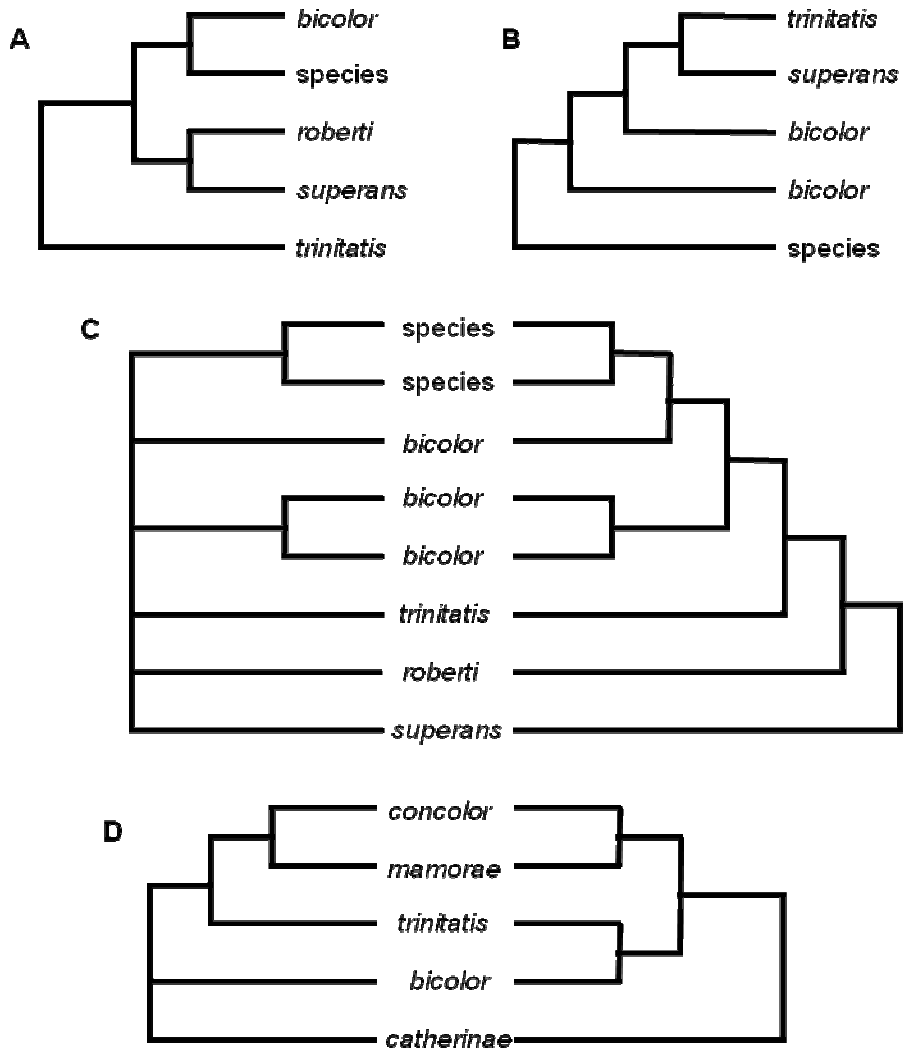

Figura 3 – Hipóteses de relações filogenéticas entre espécies de *Oecomys* propostos em relevantes estudos filogenéticos com base em dados moleculares e morfológicos. **(A)** Máxima parcimônia com base em 801 pb de citocromo-*b* sobre a relação filogenética de algumas espécies de roedores orizomíneos (PATTON e DA SILVA, 1995; adaptado da figura 9). **(B)** Análise com base em 801 pb de citocromo-*b* sobre a relação filogenética entre sigmodontíneos da América do Sul (SMITH e PATTON, 1999; adaptado da figura 2). Consenso de duas árvores de máxima parcimônia com todos os sítios com peso igual e 556 sítios informativos para parcimônia; o grupo externo foram sete espécies de neotomíneos da América do Norte. **(C)** Análise realizada com 801 pb de citocromo-*b* sobre as relações filogenéticas dentre os orizomíneos (ANDRADE e BONVINCINO, 2003; adaptado da figura 4). O cladograma da esquerda mostra o consenso estrito de três árvores mais parcimoniosas com as tranversões com peso cinco vezes maior que as transições. O cladograma da direita mostra a árvore de máxima verossimilhança com as tranversões com peso cinco vezes maior que as transições. *Neotoma albigula* e *Scotinomys teguina* foram usadas como grupo externo. **(D)** Máxima parcimônia das relações filogenéticas entre os orizomíneos com base em 99 caracteres morfológicos e 1266 pb do primeiro éxons do IRBP (WEKSLER, 2006; adaptado das figuras 34-39). O cladograma da esquerda mostra o consenso estrito de quatro árvores com comprimento mínimo a utilizando apenas seqüências de IRBP com 204 caracteres informativos para parcimônia. O cladograma da direita mostra a topologia encontrada tanto para caracteres morfológicos apenas quanto para dados combinados com caracteres polimórficos como ordenados ou compostos.

A filogenia mais abrangente atualmente, proposta por Weksler (2006) utilizando 99 caracteres morfológicos e 1266 pb do primeiro éxon do gene IRBP (Figura 3D), incluiu cinco espécies de do gênero, *Oecomys bicolor, O. catherinae, O. concolor, O. mamorae* e *O. trinitatis*. De acordo com a árvore de dados morfológicos e moleculares combinados *O. bicolor* e *O. trinitatis* formam um clado, assim como *O. concolor* e *O. mamorae*, e *O. catherinae* aparece como táxon mais basal. Entretanto, a topologia encontrada utilizando apenas dados moleculares apontou que apenas *O. concolor* e *O. mamorae* formam um clado tendo *O. trinitatis* como táxon mais proximamente relacionado, e a relação destas espécies com *O. bicolor* e *O.catherinae* indefinida.

No primeiro estudo citogenético amplo sobre os roedores orizomíneos, Gardner e Patton (1976) ressaltaram que *Oecomys* deveria ser considerado um gênero à parte de *Oryzomys*, pois as espécies do primeiro gênero apresentaram cariótipos bem diferentes das espécies de *Oryzomys* do segundo. Além disso, o estudo identificou três populações dentro de *Oecomys* com cariótipos bem diferenciados, uma relacionada a *O. bicolor* (2n=80, NA=134 ou 136) e duas relacionadas a *O. concolor* (2n=80, NA=112; 2n=60, NA=62), seguindo a nomenclatura proposta por Hershkovitz (1960).

Trabalhos recentes indicam que a diversidade cariotípica neste gênero é maior do que a encontrada por Gardner e Patton em 1976 (PATTON *et al.*, 2000; ANDRADE e BONVINCINO, 2003). No entanto, apenas sete espécies contam com o cariótipo descrito, sendo que duas delas representam espécies novas, ainda não nomeadas (Tabela 2).

Tabela 2 – Cariótipos já descritos para espécies do gênero *Oecomys*. Legenda: (**2n**) número diplóide, (**NA**) número fundamental, (**1**) Gardner e Patton, 1976, (**2**) Patton *et al.*, 2000, (**3**) Andrade e Bonvincino, 2003. Adaptado de Andrade e Bonvincino (2003).

Táxon	2n	NA	Referência
Oecomys sp.	86	98	2
Oecomys sp.	72	90	3
Oecomys bicolor	80	134-136	1
Oecomys bicolor	80	140	2
Oecomys concolor	60	62	1, 2, 3
Oecomys roberti	80	114	2
Oecomys superans	80	108	1, 2, 3
Oecomys trinitatis	58	96	2

Os trabalhos de Patton *et al.* (2000) e Voss *et al.* (2001) são exemplos de como a diversidade específica deste gênero foi subestimada na revisão feita por Hershkovitz (1960),

que reconheceu apenas duas espécies politípicas. Desde esta revisão, seis subespécies foram elevadas ao nível de espécie e oito táxons nominais foram revalidados (MUSSER e CARLETON, 1993, 2005; VOSS *et al.*, 2001). Ademais, duas novas espécies (*Oecomys cleberi* e *O. sydandersoni*) foram descritas (LOCKS, 1981; CARLETON *et al.*, 2009) e uma outra espécie nova foi registrada porém não nomeada (PATTON *et al*., 2000). Além disso, trabalhos que envolvem análises moleculares e cariotípicas também têm demonstrado que há uma maior diversidade de espécies do que a atualmente documentada (GARDNER e PATTON, 1976; SMITH e PATTON, 1999; PATTON *et al.*, 2000; ANDRADE e BONVINCINO, 2003).

Com 48 táxons nominais disponíveis e sem revisão taxonômica recente, não se conhece de maneira satisfatória a riqueza de espécies dentro do gênero *Oecomys,* tornando a identificação em nível específico uma tarefa difícil e improdutiva. É evidente que uma forma de solucionar estes problemas seja estudar a variação morfológica e a diversidade molecular e citogenética dentro de cada espécie, e assim conseguir delimitar as espécies dentro do gênero. Desse modo, este trabalho buscou caracterizar a variação morfológica e diversidade molecular das espécies com ocorrência na Amazônia oriental brasileira (*Oecomys auyantepui*, *O. bicolor*, *O. cleberi*, *O. catherinae*, *O. paricola, O. rex* e *O. rutilus*), além de outras quatro formas que podem representar tanto espécies novas como espécies já descritas, porém inválidas na forma de sinônimos (*Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C e *Oecomys* sp. D). Para isto, empregamos análises filogenéticas baseadas no gene mitocondrial citocromo-*b* com a finalidade de definir clados que representem espécies na Amazônia oriental brasileira, descrevemos a morfologia externa e craniana das espécies reconhecidas e avaliamos a variação morfológica ontogenética e sexual das mesmas, investigando se existe congruência entre a variação genética e morfológica. Foi adotado o Conceito Filogenético de Espécie ampliado por Nixon e Wheeler (1990), no qual uma espécie é definida como a menor agregação de populações ou linhagens diagnosticável por uma combinação única de estados de caracteres em indivíduos comparáveis (semaforontes) (DE PINNA, 1999).

Os métodos e os resultados encontrados neste estudo são apresentados detalhadamente a seguir, em formato de artigo científico a ser submetido à revista *Zootaxa*.

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Zootaxa

Morphological and molecular diversity in the species of *Oecomys* Thomas, 1906 (Rodentia: Cricetidae) from eastern Amazon in Brazil

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ABSTRACT

The arboreal rice rats, genus *Oecomys*, are distributed in tropical and subtropical areas from Central and South America, with 17 currently recognized species and another two species already described in earlier studies but still unnamed. Six of these species are expected to occur in eastern Brazilian Amazon. Because defining the species limits inside *Oecomys* based only on morphological characters is a complicated task, many nominal taxa have already been associated to the genus, and different taxonomic arrangements have been proposed by specialists. Despite of this taxonomic instability, there is only one taxonomic review for the genus carried out 50 years ago, in which only two polytypical species were recognized. However, several recent studies based on morphological, molecular and karyotypical data have been showing that the species diversity inside *Oecomys* is largely underestimated, resulting in recent descriptions of new taxa or revalidation of previously synonymized species. This work aimed to assess the species diversity inside this genus in the eastern Brazilian Amazon by investigating the molecular and morphological variation in regional specimens. We employed phylogenetic analysis based on cytochrome-*b* in order to define clades that may represent species, and described the external and cranial morphology of these species. As a result, we recognized 11 species in the eastern Amazonian forest in Brazil, of which five are already expected to occur in this area (*Oecomys auyantepui*, *O. bicolor*, *O. paricola*, *O. rex*, and *O. rutilus*), two are recorded for the first time in Amazonia (*Oecomys catherinae* and *O. cleberi*), and four are either new or not currently recognized species (i.e. synonyms), herein referred as *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C, and *Oecomys* sp. D. Moreover, we suggest that *Oecomys bicolor* is a species complex, based in the high nucleotide divergence we found (7.5 %), corroborating previous molecular studies. We observed sexual dimorphism and ontogenetic variation on cranial morphometry in *Oecomys paricola*, and for comparison purposes we treated all other species herein studied as exhibiting this kind of dimorphism. We also suggest a phylogenetic hypothesis among the species of this genus based on 653 bp of cytochrome-*b*. This is the most comprehensive phylogeny for *Oecomys* published to date, due to the great number of species included in the analysis (11 of the 16 currently recognized species plus seven probably new species), and the wide-ranging geographic area included in our sample.

INTRODUCTION

The arboreal rice rats, genus *Oecomys* Thomas, 1906, are attractive red-toned mice distributed in tropical and subtropical areas from Central and South America, including Costa Rica, Trinidad, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Guyana, French Guyana, Surinam and Brazil (Musser & Carleton 2005; Carleton *et al.* 2009).

Most nominal taxa associated to *Oecomys* today were originally described under the genera *Oryzomys* or *Rhipidomys*. Based on gross morphology of skull, broad feet with digit V reaching at least the first phalanx of digit IV, and tail with the base covered by body pelage and a pencil on tip, Thomas (1906) created the subgenus *Oecomys* to group *Hesperomys bicolor* Tomes, 1860 and some arboreal rodents previously described under *Rhipidomys* (*dryas* Thomas, 1900; *phaeotis* Thomas, 1901; *benevolens* Thomas, 1901; *rosilla* Thomas, 1904; *paricola* Thomas, 1904; *marmosurus* Thomas, 1899; *mamorae* Thomas, 1906; and *roberti* Thomas, 1904). The newly created subgenus was associated to *Oryzomys* by Thomas (1906), based on the long palate (that extends some distance behind M3) with posterolateral pits and the number of mammae (eight in *Oryzomys*). Other nominal taxa already described to then and currently assigned to *Oecomys*, like *concolor* Wagner, 1845, *speciosus* J.A. Allen & Chapman, 1893, *trinitatis* J.A. Allen & Chapman, 1893, *flavicans* Thomas, 1894, *subluteus* Thomas, 1898, *fulviventer* J.A. Allen, 1899, *palmarius* J.A. Allen, 1899, *trichurus* J.A. Allen, 1899, *tectus* Thomas, 1901, and *klagesi* J.A. Allen, 1904 were not immediately included in *Oecomys* by Thomas (1906).

In 1909, Thomas recognized *Oecomys* as a valid genus, adding the hardly forward project of outer plate of the anterior zygoma-root (versus the strongly projection in *Oryzomys*) as a diagnostic character of the genus. Thereafter, some authors treated *Oecomys* alternatively as a subgenus (Ellerman 1941; Cabrera 1960) or as full genus (Anthony 1921; Gyldenstope 1932) until Hershkovitz's (1960) review stabilized its rank as a subgenus for almost two decades. More recently, systematists have acknowledged the morphological, karyotypic and genetically distinctiveness of *Oecomys* at the generic level (Gardner & Patton 1976; Carleton & Musser 1984; Reig 1984, 1986; Smith & Patton 1999; Andrades-Miranda *et al.* 2001; Weksler 2003).

Hershkovitz (1960) published the only taxonomic review available for the genus. He consolidated 25 species into only two, *O. bicolor* and *O. concolor*, based on a few

morphological features, like body size, proportion of foot size in relation to body size, and development degree of supraorbital ridges. In the same paper, Hershkovitz recognized four subspecies associated to the former species (*bicolor* Tomes, 1860; *phaeotis* Thomas, 1901; *trabeatus* G.M. Allen & Barbour, 1923; and *occidentalis* Hershkovitz, 1960) and five subspecies associated to the latter (*concolor* Wagner, 1845; *superans* Thomas, 1911; *speciosus* J.A. Allen & Chapman, 1823; *roberti* Thomas, 1904; and *bahiensis* Hershkovitz, 1960). Authors that investigated the taxonomic diversity in *Oecomys*, after Hershkovitz's revision, disagreed with the specific arrangement proposed by him and recognized at least four species in sympatry or close parapatry (Voss & Emmons 1996: Appendix 8; Patton *et al.* 2000; Voss *et al.* 2001). In a recent taxonomic compendium, Musser & Carleton (2005) recognized 15 valid species, two of which (*O. bicolor* and *O. trinitatis*) may be composite. Most recently, Carleton *et al*. (2009) described a new species from Bolivia, totaling 16 species currently recognized and 48 nominal taxa associated with *Oecomys* (Appendix 2).

According to Johns & Avise (1998) and Avise & Walker (1999), the mitochondrial cytochrome-b gene shows a high level of congruence with species limits based on classical taxonomic studies, which means that it has great significance to biodiversity investigations (Bradley & Baker 2001). In fact, very important studies involving phylogenies of sigmodontinae rodents are based on the cytochrome-b gene as molecular marker (Smith & Patton 1991, 1993, 1999; Patton *et al*. 2000; Andrade & Bonvincino 2003; D'Elia 2003; Miranda *et al.* 2007; D'Elia *et al*. 2008; Catzeflis & Tilak 2009). Most of them tried to elucidate the relationships and radiation of South American cricetids (Smith & Patton 1991, 1993, 1999; D'Elia 2003; Weksler 2003, 2006), and their results corroborates the monophyly of the tribe Oryzomyini and the genera it contains, including *Oecomys*. However, phylogenetic relationships inside the genus *Oecomys* are poorly known (Figure 1), based on five molecular (Patton & Da Silva 1995; Smith & Patton 1999; Patton *et al.* 2000; Andrade & Bonvincino 2003; Weksler 2003) and one combined (molecular and morphological) data studies (Weksler 2006), all of which include no more than 15 specimens belonging to at most five species.

As shown above, the taxonomic diversity and species relationships within *Oecomys* are poorly known, and identification at the species level is frequently a troublesome and unreliable task. Obviously, a starting point to solve these problems is to investigate the molecular and karyotypical diversity and morphological variation in large and geographically distinct samples of *Oecomys* specimens. In this sense, we aimed to assess the species diversity

in *Oecomys* from the eastern Brazilian Amazon by investigating the molecular and morphological variation in regional specimens. Herein, we present the most comprehensive phylogeny for *Oecomys* published to date, due to the great number of species included in the analysis and the wide-ranging geographic area included in our sample. We also provide morphological descriptions and comparisons for the recognized taxa, as well as distributional maps.

MATERIAL AND METHODS

ANALYZED SPECIMENS

We analyzed 467 *Oecomys* specimens, including skulls, dry skins and fluid preserved specimens (Appendix 2) from the eastern Amazon region, particularly from the Brazilian states of Amapá, Pará, and Mato Grosso, deposited in the following institutions: Museu Paraense Emílio Goeldi (MPEG); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade de São Paulo (MZUSP); and Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (IEPA). Specimens temporarily housed in the Universidade Federal do Pará (UFPA) that will be deposited in the MPEG were also analyzed. In this report, they are identified by the acronym of field expeditions BAR (Barcarena Project).

Specimens' localities were obtained from labels and collection registration books. Geographic coordinates were defined using maps, catalogs, gazetteers (Hershkovitz 1960; Paynter & Traylor 1991; Vanzolini 1992; Gardner 2007), internet sites (National Geospatial-Intelligence Agency - GEONET) and, when possible, directly from collectors. Distributional maps were made using ArcGis 9.3 software.

For morphological and morphometric comparisons, localities were grouped together according to some of the recognized Amazonian centers of endemism (Silva *et al*. 2005), as follows: Guiana – northern Amazon River; Belém – eastern Tocantins River; Xingú – between the rivers Xingú and Tocantins; Marajó – Marajó Island; Tapajós – between the rivers Tapajós and Xingú; and Rondônia – between the rivers Madeira and Tapajós.

MOLECULAR ANALYSIS

We extracted 653 bp of cytochrome-b sequences of 180 muscular tissue ethanol-preserved samples of *Oecomys* (Appendix 3). However, we used 102 sequences in our phylogenetic analysis, restricting our sample to unique sequences (haplotypes) and at most three specimens per locality for each morpho-species. We also used eight *Oecomys* sequences available in GenBank (Table 1), and one sequence of *Euryoryzomys macconnelli* (LGV151), plus one GenBank sequence of *Hylaeamys megacephalus* (AY275124) as the outgroups in the phylogenetic analysis.

DNA extraction was made using phenol-chloroform and proteinaseK-RNAse protocol (Sambrook *et al*. 1989). Sequences were amplified with polymerase chain reaction (PCR) with primers MVZ05 5'-CGAAGCTTGATATGAAAAACCATCGTTG-3' and MVZ16 5'AAATAGGAARTATCAYTCTGGTTTRAT-3' (Smith & Patton 1993). Amplification protocol consisted in initial denaturation at 94ºC by 3 minutes, followed by 35 cycles of 30 seconds of denaturation at 94ºC, 1 minute of annealing at 45ºC and 2 minutes of extension at 72ºC, with a final extension at 72ºC by 7 minutes.

Sequences were edited on BioEdit 7.0.5.2 (Hall 1999) and aligned on ClustalX 2.0.9 (Larkin *et al.* 2007), following proposed parameters by Schneider (2006), with posterior manual rectification on BioEdit. Sequences saturation was verified on DAMBE 5.0.59 software (Xia & Xie 2001), and then we proceeded with the following analysis. Using MrModeltest 2.3 (Nylander 2004) on PAUP 4.0*, we found GTR+I+G with a substitution rate equal to 6, gamma distribution parameter equal to 0.9321, and invariable sites proportion equal to 0.5223 as the best evolutive model to our sequences. Neighbor Joining analysis was conducted on MEGA 4.0 (Tamura *et al.* 2007) with Kimura-2 parameter (Kimura 1980) and gamma distribution parameter equal to 0.9321. Bayesian analysis was conducted on MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) using the evolutionary model described above, two runs, four chains, 3 millions generations and sample frequency equal to 100. Maximum Likelihood was conducted on PhyML site (Guindon & Gascuel 2003), using the above referred evolutive model, a BioNJ initial tree and 1000 replicates in bootstrap (Felsenstein 1985) for clade support. Maximum Parsimony was conducted on PAUP*4.0, and the best tree was found with a heuristic search.

Estimates of evolutionary divergence over sequence pairs between and within *Oecomys* species and populations were conducted using the Kimura 2-parameter model in MEGA 4.0 (Kimura 1980; Tamura *et al.* 2007) considering different patterns of nucleotide substitutions among lineages. The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.9321). All codon positions were included and all positions containing alignment gaps and missing data were eliminated only in pair wise sequence comparisons.

AGE CRITERIA

In order to perform more accurate morphological and morphometric comparisons, specimens with complete dentition (M3 present) were initially classified into five age classes based on the eruption pattern and the differential wear of occlusal surface of superior molars, following Voss (1991) and Brandt & Pessôa (1994). However, an one-way ANOVA test performed with specimens of *Oecomys paricola* from the Xingú center of endemism plus the Marajó Island (47 males and 22 females) showed that age classes 2 and 3 were not significantly distinct ($F = 1.46$; $p = 0.22$), as well as age classes 4 and 5 ($F = 5.01$; $p = 0.34$). By contrast, age classes 3 and 4 appeared as significantly distinct classes ($F = 2.89$; $p = 0.002$). As a result, in this report we recognize only three age classes, defined as follows.

Age class 1: M3 incompletely erupted or unworn.
Age class 2: Occlusal surface exhibiting slight to moderate wear, but still tubercular; mesoflexus and paraflexus of M1 and M2 sometimes as enamel islands; all M3 flexus, except paraflexus, obliterated and sometimes as enamel islands.
Age class 3: Occlusal surface flat or concave; paraflexus, metaflexus, protoflexus, and hypoflexus as the only flexus present in M1 and M2; other flexus, when present, are just enamel islands; paraflexus of M3 always as an enamel island, or totally absent.

MORPHOLOGICAL ANALYSIS

We evaluated morphological characters present on skins and skulls that could be used to segregate groups of individuals. Comparisons between specimens were made considering sex and age classes. For anatomical nomenclature we followed Pocock (1914), Hershkovitz (1962, 1977), Carleton & Musser (1984, 1989) and Voss (1988) concerning external

morphology, Reig (1977), Hershkovitz (1993), and Weksler (2006) concerning dental morphology, and McDowell (1958), Hershkovitz (1962), Wahlert (1974), Carleton & Musser (1984, 1989), Voss (1988), Steppan (1995) and Weksler (2006) in respect to cranial morphology.

MORPHOMETRIC ANALYSIS

The following external measurements were obtained directly from specimens' labels and used only for descriptive analysis: head and body length (HBL), tail length (TL), foot length (FL), ear length (EL) and weight (W).

We obtained 30 craniodental measurements from 345 specimens using a digital caliper to the nearest 0.01 mm while skulls were examined under a stereomicroscope. These craniodental measurements are defined as follows.

Braincase Height (BH): From basisphenoid-basioccipital suture to frontal-parietal suture on midline.

Breadth of Incisive Foramen (BIF): Greatest transverse dimension across both incisive foramina.

Breadth of Incisor (BI): Distance between internal and external curvature of one upper incisor.

Breadth of Interparietal (BIP): Greatest breadth of interparietal bone.

Breadth of M1 (BM1): Greatest crown breadth of the first upper molar (M1).

Breadth of m1 (Bm1): Greatest crown breadth of the first lower molar (m1).

Breadth of Palatal Bridge (BPB): Measured between the protocones of the right and left M1.

Breadth of Palate at Rostrum (BPR): Measured between most posterior lower edges of infraorbital foramina on ventral side of skull.

Breadth of Zygomatic Plate (BZP): Least distance between anterior and posterior edges of the zygomatic plate.

Bullar Breadth (BB): Distance between anterior open of carotid foramen to ectotimpanic dorsal process.

Condylo-incisive Length (CIL): From the greater curvature of one upper incisor to the articular surface of the condyle on the same side.

Condylo-zygomatic Length (CZL): From the most anterior point in anterior edge of zygomatic plate to the articular surface of the condyle on the same side.
Least Condyloid-Incisor Breadth (LCIB): Greatest distance from the lower incisor base to the posterior margin of the condyloid process on the same side.
Least Interorbital Breadth (LIB): Least distance across the frontal bones between the orbital fossa.
Length of Diastema (LD): From the crown of the first cheektooth to the less curvature of the incisor on the same side.
Length of Incisive Foramen (LIF): Greatest anterior-posterior dimension of one incisive foramen.
Length of Interparietal (LIP): Greatest length of interparietal bone.
Length of Lower Diastema (LLD): From the crown of the first cheektooth to the less curvature of the incisor on the same side.
Length of Lower Molars (LLM): Crown length from m1 to m3.
Length of Molars (LM): Crown length from M1 to M3.
Length of Nasals (LN): Greatest anterior-posterior dimension of one nasal bone.
Length of Palatal Bridge (LPB): Midline distance from posterior margin of incisive foramina to anterior margin of mesopterygoid fossa.
Mandible Height (MH): From the angular process to the condyloid process on the same side.
Mastoid Breadth (MB): Distance across cranium at mastoid processes.
Occipital Condyle Breadth (OCB): Outside distance between occipital condyles.
Orbital Length (OL): Internal distance between anterior and posterior margins of the orbit.
Rostral Breadth (RB): Distance between the outside margins of nasolachrymal capsule.
Rostral Length (RL): Diagonal measurement taken from anterior margin of orbit to anterior margin of the nasal bone on the same side.
Zygomatic Breadth (ZB): Greatest transverse dimension across the squamosal zygomatic processes.
Zygomatic Length (ZL): From the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic.

Descriptive statistics were calculated for each species using age classes 2 and 3. Data set were $\log_{10}$ transformed to reduce the size effect and normalize data. Sexual dimorphism was tested by T-Test with Hotteling's Multivariate Analysis with specimens of *Oecomys paricola* from the Xingu center of endemism (between the rivers Xingu and Tocantins) plus

the Marajó Island (47 males and 22 females). After that, we performed a Factorial Analysis to detect correlation among variables with measurements of *O. paricola* males from the age class 2 (n = 41). This analysis showed that 14 variables (BH, BI, BPR, CIL, CZL, LCIB, LD, LIF, LLD, MH, OL, RL, ZB, ZL) were highly correlated (> 70 %) to at least one of the remaining 16 variables (BB, BIF, BIP, BM1, Bm1, BPB, BZP, LIB, LIP, LLM, LM, LN, LPB, MB, OCB, RB). Consequently, we excluded the former 14 variables cited above to the subsequent analysis. A Discriminant Analysis was performed to verify if morphometric data were congruent with molecular and morphological data. All analyses were performed on StatSoft STATISTICA 8.0 and PAST 4.0 (Hammer *et al*. 2001) statistical packages, with significance level at 5 %.

Species Concept

In order to define the species limits in this study, we followed the phylogenetic species concept of Nixon & Wheeler (1990), wherein a species is defined as the smaller group of population or lineages that can be diagnosed by a unique combination of character states among comparable individuals (De Pinna, 1999). We also contrasted morphological and molecular data in order to find the strict combination of morphological characters and molecular distances to define the species. Since we did not have access to typespecimens, we named species according to the original descriptions from the literature and descriptions provided by Patton *et al.* (2000) and Voss *et al.* (2001).

Results and Discussion

Molecular Analyses

All phylogenetic analyses (Neighbor Joining - NJ, Bayesian Inference - BI, Maximum Likelihood – ML and Maximum Parsimony – MP; Figures 2 – 5, respectively) yielded the same groups, but the relationships among those groups were uncertain. After a detailed morphological analysis, we were able to associate 18 monophyletic groups to distinct species of *Oecomys*, namely *Oecomys auyantepui*, *O. bicolor*, *O. bicolor* (Peru), *O. cleberi*, *O. catherinae*, *O. paricola*, *O. rex*, *O. roberti*, *O. rutilus*, *Oecomys* sp. (which refers to the specimen MZUSP 29530 that we did not examine the voucher), *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C, *Oecomys* sp. D, *Oecomys* sp. (Corumbá, Mato Grosso do Sul; Andrade &

Bonvincino 2003; probably *O. mamorae*), *Oecomys* sp.n. (Juruá River; Patton *et al.* 2000), *O. superans*, and *O. trinitatis*. Eleven of these clades occur in the eastern Amazonian region (Guiana, Belém, Xingú, Tapajós and Rondônia centers of endemism), five of which represents new or not currently recognized species.

Oecomys rex and *O. catherinae* appeared as sister-taxa in all analyses (clade A), forming a group with low nodal support in BI (93 %) and in NJ and ML analyses (66 % and 59 %, respectively). This group was sister to all other *Oecomys* species in NJ, BI and ML analysis, and to all species except *O. auyantepui* and *O. rutilus* in MP analysis. *Oecomys paricola* and *Oecomys* sp. also appeared as sister-taxa (clade B; nodal support: 99 % in NJ, 100 % in BI, and 100 % in ML). This clade was sister to all *Oecomys* species, except clade A, *O. rutilus* and *O. auyantepui* in BI, ML and MP, whereas in NJ the clade B was placed as sister to *O. auyantepui*, and *O. rutilus* successively. *Oecomys bicolor* (Peru) and *Oecomys* sp. D always appeared as sister-taxa (clade C) but there is no nodal support (< 50 % in NJ, 79 % in BI, and < 50 % in ML).

Another three monophyletic groups of species were recovered in all phylogenetic analyses, but internal relationships among species were uncertain. The first was composed of clade C, *Oecomys bicolor*, and *O. cleberi* (clade D); the second was composed of *Oecomys roberti*, *Oecomys* sp. B, and *Oecomys* sp. C (clade E); and the third was composed of clade D, clade E, *Oecomys* sp. A, *Oecomys* sp. (Corumbá), *Oecomys* sp. (Juruá), *O. superans*, and *O. trinitatis* (clade F).

The clade D was well supported in BI, with 100 % of nodal support, as a politomy among *Oecomys bicolor, O. cleberi* and clade C. In NJ this clade is supported by 70 % of bootstrap, with clade C as the sister group of *O. bicolor* (less than 50 % of nodal support), and *O. cleberi* as the sister taxa to the group. MP consensus tree showed the same topology of NJ analysis. In ML all nodal supports were less than 50 %, and *Oecomys bicolor* appeared as sister-taxa of *O. cleberi*.

The clade E was well supported in all analysis (99 % in BI, 76 % in ML and 81 % in NJ). In BI and ML, *O. roberti* and *Oecomys* sp. C appeared as sister-taxa (nodal support of 67 % in BI and 58 % in ML), and both forming the sister-taxa of *Oecomys* sp. B. In NJ and MP, *O. roberti* was basally placed to *Oecomys* sp. C plus *Oecomys* sp. B, and this latter clade showed less than 50 % of NJ bootstrap.

The clade F had more than 50 % of nodal support in all analysis (91 % in BI, 52 % in ML and 63 % in NJ); however, relationships among species of this clade varied considerably, and all internal clades were barely supported, usually with less than 50 % of nodal support. The Bayesian Inference was the most consensual phylogeny, and showed this clade as a politomy (nodal support: 69 %) among the clades *Oecomys* sp. (Juruá) + *Oecomys* sp. (Corumbá), *Oecomys* sp. A, and clade D. In this phylogeny, the species described by Patton *et al.* (2000) from Juruá River and the species described by Andrade & Bonvincino (2003) from Corumbá, Mato Grosso, appeared as sister-taxa with 64 % of nodal support, and this topology involving these two taxa was corroborated in MP and NJ analysis.

All phylogenetic studies of *Oecomys* based on cytochrome-b gene included only species of our clade F, which are *Oecomys bicolor*, *O. roberti*, *O. superans*, *O. trinitatis*, *Oecomys* sp. from Corumbá, and *Oecomys* sp. from Juruá River (Figure 1; Patton & Da Silva 1995; Smith & Patton 1999; Patton *et al.* 2000; Andrade & Bonvincino 2003). The sequences of *Oecomys bicolor*, *O. roberti*, *O. superans*, *O. trinitatis*, and *Oecomys* sp. employed by Patton & Da Silva (1995) and Patton *et al.* (2000) were obtained from specimens collected along the Juruá River. Smith & Patton (1999) used sequences of specimens collected in some localities in Peru. Andrade & Bonvincino (2003) used the sequences from the Juruá River, one sequence of *Oecomys bicolor* from Peru used by Smith & Patton (1999; the same used by us; Table 1) and sequences of *Oecomys* sp. from Corumbá, Mato Grosso. In all these studies, the clade composed of these samples was strongly supported, which corroborates the monophyly of the genus. However, the relationships among the species were uncertain or barely supported, just like in our phylogenies presented here. The phylogeny suggested by Weksler (2006; Figure 1D on this report) based on IRBP gene and morphological data included *O. bicolor*, *O. catherinae*, *Oecomys concolor*, *O. mamorae*, and *O. trinitatis*, and showed *O. catherinae* sister to all other taxa. *Oecomys trinitatis* and *O. bicolor* appeared as sister-taxa, as well as *O. concolor* and *O. mamorae*. Our phylogenies corroborate the fact that *O. catherinae* is a basal taxa in relation to the other species studied by Weksler (2006), and that *O. trinitatis* and *O. bicolor* are closely related since both are part of our clade F. We are not able to discuss the relationship between *O. concolor* and *O. mamorae* because we did not include the former species in our analysis.

The phylogenies presented by Smith & Patton (1999) and Andrade & Bonvincino (2003) suggested that *Oecomys bicolor* is a species complex. Our results corroborate that hypothesis, since the specimens herein identified as *O. bicolor* from Rondonia and Guiana

centers of endemism, which are the same specimens studied by Patton & Da Silva (1995) and Patton *et al.* (2000) exhibit 7.5 % of nucleotide divergence from the specimens of *Oecomys bicolor* from Peru identified by Smith & Patton (1999). Besides, *O. bicolor* appeared as a paraphyletic species in all of our analysis, just like the parsimony analysis of Smith & Patton (1999). Ten nominal taxa have already been associated to *O. bicolor*, and in the absence of a thorough taxonomic revision of *Oecomys* since Hershkovitz (1960), some of them may represent valid species.

Three species were represented by more than two sequences from specimens limited by the main Amazonian rivers in our phylogenetic analysis: *Oecomys catherinae*, *Oecomys* sp. B, and *O. bicolor*. Despite the fact that in NJ analysis the population of *O. bicolor* from Rondônia appeared separated in two ((Guiana, Rondônia), Rondônia), this clade was stable in all analysis (nodal support 100 % in BI, 71 % in ML, < 50 % in NJ) and the population from Juruá (represented by one specimen) was always sister to Guiana and Rondônia specimens (nodal support: 75 % in BI, 53 % in ML, 62 % in NJ). *Oecomys catherinae* had three populations represented in this report (Atlantic Forest, Rondônia and Xingu). In MP and NJ, specimens from the Atlantic Forest were closely related to those from Xingu (89 % of nodal support in NJ), and specimens from Rondônia were basally placed to them (99 % of nodal support in NJ). In ML, specimens from Xingu were closely related to those from Rondônia (less than 50 % of nodal support), and specimens from the Atlantic Forest were basally placed, with 98 % of nodal support. In BI, all populations appeared as a politomy (nodal support; 100 %). *Oecomys* sp. B also had three populations represented in our analysis (Guiana, Belém and Xingú) (nodal support: 100 % in BI, 92 % in ML, < 50 % in NJ). In BI and ML, specimens from Xingu were basally placed to Guiana and Belém specimens, this last clade with low nodal support, 51 % in BI and 53 % in ML. In MP and NJ, specimens from Guiana were basally placed to Belém and Xingu specimens, all with less than 50 % of nodal support.

The intrapopulational genetic divergences in our data set range from 0.3 % to 2.1 %. The intraspecific mean divergences ranged from 1.0 % to 2.1 % in species with only one population represented, and from 2.6 % to 3.9 % in species with two or more populations represented (Table 2). Evolutionary divergences between sister-species ranged from 6.1 % (between *Oecomys* sp. and *O. paricola*) to 9.6 % (between *Oecomys catherinae* and *O. rex*). The intrageneric evolutionary divergences ranged from 6.1 % to 17 % (Table 3).

Bradley & Baker (2001) tested whether levels of cytochrome-*b* sequence divergences can be used to identify species-level differentiation under the framework of the Genetic Species Concept, using bats and rodent species as models. For rodents they found that values of intrapopulational divergences vary from 0 - 0.53 %, intraspecific divergence from 0 - 6.29 %, between sister-species from 2.7 - 19.23 %, and intrageneric divergence from 2.23 - 21.97 %. Other molecular studies for sigmodontinae rodents show values that range from 0 – 3.87 % for intrapopulational divergence, from 0 – 11.37 % for intraspecific divergence, about 8.4 % for sister-species divergence, and from 1.23 – 21 % for intrageneric divergence (Smith & Patton 1991, 1993, 1999; Patton *et al*. 2000; Andrade & Bonvincino 2003; D'Elia 2003; Miranda *et al.* 2007; D'Elia *et al*. 2008; Catzeflis & Tilak 2009). Particularly for *Oecomys*, there are no intrapopulational and sister-species divergences published, but intraspecific divergences range from 0 – 10.3 %, and intrageneric divergence range from 7 – 12 % (Smith & Patton 1999; Patton *et al.* 2000; Andrade & Bonvincino 2003).

The intraspecific evolutionary divergences found by us are lower than divergences registered for *Oecomys* in the literature, and the range of our intrageneric divergences is greater than those from the literature, but both lie inside those observed for other Sigmodontinae rodents. It is important to mention that this is the first molecular study with cytochrome-*b* for *Oecomys* that employ a large number of haplotypes (n=102) and species. Previous molecular studies employed five haplotypes for five species (Patton & Da Silva 1995), 15 haplotypes for four species (Smith & Patton 1999), 11 haplotypes for five species (Patton *et al.* 2000), and eight haplotypes for five species (Andrade & Bonvincino 2003). Therefore we provide here the most comprehensive phylogenetic analysis of *Oecomys* using cytochrome-*b* as molecular marker.

MORPHOLOGICAL ANALYSIS

Regardless the phylogenetic relationships among the eleven species from eastern Amazon forest discussed above, we can roughly separate them in two groups of species on the basis of external morphology in order to facilitate comparisons among species herein recognized and identification of specimens from the studied area. The first group can be characterized by small to intermediate body size and mainly pure white hairs on ventral pelage (Tables 4 – 5), pooling together *Oecomys bicolor*, *O. cleberi*, *O. rutilus*, *Oecomys* sp.

A, and *Oecomys* sp. D. By contrast, the second group exhibits intermediate to large body size and mainly gray-based hairs on ventral pelage (Tables 6 – 7), pooling together *O. auyantepui*, *O. paricola*, *O. catherinae*, *O. rex*, *Oecomys* sp. B, and *Oecomys* sp. C.

The first group occurs in eastern Amazon forest, except in Marajó Island and on the eastern margin of the Tocantins River. *Oecomys cleberi* is the only species of this group to occur in the Xingu region, and compared to other species from the same group, it is readily distinguished by its short tail (about 101 % of head and body length) and a bright yellow line separating dorsal and ventral fur. *Oecomys* sp. D is the only species of small bodied *Oecomys* distributed at the Tapajós region, and compared to other species of the group it is easily identified by being the smallest species of *Oecomys*, (see morphometric analysis), exhibiting longer scale hairs (more than 3 scale rows in length), in tail, orange hairs on inner surface of ears, bright brownish orange dorsal fur coloration, and entirely white hairs on ventral pelage.

Oecomys bicolor and *O. rutilus* occur in sympatry at the Guiana region, but despite the similar coloration of ventral pelage, both species can be easily separated externally by the pencil length, which is less than 5 mm in *O. bicolor* and about 9 mm in *O. rutilus*; length and shape of hindfoot, which are small and broad (about 15 % of head and body length) with *squamae* in plantar surface in the former, and large and narrow (about 23 % of head and body length) with smooth plantar surface in the latter; dorsal body fur is shorter (about 6 mm), bright brownish orange in *O. bicolor*, and longer (about 8 mm), yellowish to reddish brown colored in *O. rutilus*; the former exhibits head fur generally darker than dorsal fur, and the latter has the flank fur grayish than dorsum. Both species can also be distinguished by some craniodental characters (Table 5), as the extension ou development of supraorbital ridges, which are restricted to frontals in *Oecomys rutilus* and extended to parietals in *O. bicolor*; the length of mesopterygoid fossa, which never extends beyond the maxillary bone in *O. bicolor* but extends beyond this bone in *O. rutilus*. Additionally, in the former species the parapterygoid fossa lies at the same level of the palatine bone, whereas it is slightly under the palate level in the latter; *O. rutilus* often shows the alisphenoid strut at least in one side of the skull, and the anterior opening of the alisphenoid canal is always small, whereas in *O. bicolor* the alisphenoid strut is always absent and largethe buccinators-masticatory foramen and accessory foramen ovale are confluent; the capsular process of the lower incisor alveoli is slightly curved in *O. bicolor*, but moderately curved in *O. rutilus*; the hypoflexus in M3 is shallow in the former species, and deep in the latter; and *O. bicolor* always shows an accessory labial root in m1, whereas *O. rutilus* shows only two roots in m1.

Oecomys bicolor is also sympatrically distributed with *Oecomys* sp. A in the Rondônia region, but both species differ in many external and craniodental characters (Tables 8 – 9) and can be easily discriminated. In *O. bicolor* the central scale hair is thicker than the lateral ones, whereas in *Oecomys* sp. A all scale hairs are about the same thickness; *Oecomys* sp. A shows the most different tail color compared to all other congeneric species, covered mainly with blackish hairs and sparsely with pure white hairs. This species also shows the caudal pencil longer (about 9 mm) than *O. bicolor* (less than 5 mm); hindfoot shorter and wider (about 15 % of head and body length), with *squamae* in plantar surface in contrast to the longer and narrower hindfoot (about 23 % of head and body length), with smooth plantar surface in *O. bicolor*; dorsal body fur longer (10 mm) and dark reddish in general but bright reddish on rump, whereas in *O. bicolor* it is shorter (6 mm) and bright brownish orange. *Oecomys* sp. A is the only species of the small bodied group that shows the inner part of legs covered with gray-based hairs. Concerning craniodental morphology, *Oecomys* species A is more similar to the species of the intermediate to large bodied group, with very robust skull and large mandible. The nasal bones are long, whereas all other species of the small bodied group have short nasals; the supraorbital ridges are restricted to frontals in *Oecomys* sp. A, but extended to parietals in *O. bicolor*; the mesopterygoid fossa extends beyond the maxillary bone in the former, but never extends beyond this bone in the latter; and the parapterygoid fossa lies slightly under the palate level in *Oecomys* sp. A, whereas the fossa is about the same level of the palate bone in *O. bicolor*. In addition, *Oecomys* sp. A always shows the alisphenoid strut and exhibits small anterior opening of the alisphenoid canal, whereas in *O. bicolor* the alisphenoid strut is always absent and the anterior opening of the alisphenoid canal is large; the capsular process of the lower incisor is curved in *Oecomys* sp. A but slightly curved in *O. bicolor* ; and *Oecomys* sp. A exhibits only two roots in m1, whereas *O. bicolor* always shows an accessory labial root in m1.

The second group, which is composed of species with intermediate to large body size and mainly gray-based hairs on ventral surface, is widely distributed in eastern Amazon region, including the Marajó Island and the Belém region. *O. catherinae* is easily distinguished from other sympatric species (*O. paricola* and *Oecomys* sp. B in the Xingu center of endemism, and *Oecomys* sp. C in the Rondônia center of endemism; Tables 10 – 11) by its larger body size (Table 6); presence of *squamae* in the plantar surface, in contrast to the smooth plantar surface of the others; ventral pelage mostly consisted of dark gray-based hairs with a small pure white spot restricted to throat, in contrast to the lighter gray-based fur with

chin and throat covered with self-white hairs in *O. paricola*, *Oecomys* sp. B, and *Oecomys* sp. C; large dorsal fur (13 mm), in contrast to short dorsal fur in the other three species (9 mm); short nasal bone, instead of long nasal bones in *O. paricola*, *Oecomys* sp. B, and *Oecomys* sp. C; distinct zygomatic notch, in contrast to shallow zygomatic notch in the latter three species; supraorbital ridges strongly marked along the parietals while in the other sympatric species the supraorbital ridges are restricted to the frontals; mental foramen disposed in front of the molar tooth row and capsular process of lower incisor alveoli strongly curved, whereas the mental foramen is laterally disposed and the capsular process is slightly curved in the other three species; accessory roots in M1 and m1 in *O. catherinae* in contrast to only two roots in M1 and m1 in *O. paricola*, *Oecomys* sp. B, and *Oecomys* sp. C; and the absence of the protoflexus in M2 in *O. catherinae*, while it is present in the latter three species.

The phylogenetic hypothesis proposed in this study indicates that *Oecomys catherinae* and *Oecomys rex* are perhaps sister-taxa. Morphologically, we corroborate this hypothesis since there are many external and craniodental characters shared by these two species, such as the development of the supraorbital ridges as strongly marked ridges across the parietals, which additionally exhibit a conspicuous postorbital process in *O. rex*; the zygomatic notch very distinct, compared to other congeneric species (although shallow if compared to other Oryzomyini, such as *Euryoryzomys*); and the mental foramen disposed in front of the molar tooth row.

Besides the sympatry between *Oecomys paricola* and *O. catherinae*, the former is also sympatric with *Oecomys* sp. B, but both species can be readily differentiated by the presence of a pencil on caudal tip in *O. paricola* (absent in *Oecomys* sp. B), and the narrow hindfoot with a conspicuous spot at metatarsals in the former against broad hindfoot with no spot at metatarsals in the latter. Voss *et al.* (2001) suggested that *Oecomys paricola* and *O. auyantepui* could be sister-taxa, but in our phylogenetic analysis these species were not closely related, with 12.2 % of nucleotide divergence. However, morphological analysis showed many similar characters in both species. Indeed, a few specimens from the Xingu center of endemism and all specimens from the Marajó Island assigned to *O. paricola* are much more like *O. auyantepui* than *O. paricola* from the Belém region. But specimens from Belém (near the type locality of *O. paricola*) can be differentiated by *O. auyantepui* by a few cranial characters, such as long nasal bones, slightly developed supraorbital ridges restricted to frontals, mesopterygoid fossa never extending beyond the maxillary bone, alisphenoid strut always absent, anterior opening of the alisphenoid canal always present, subsquamosal

fenestra always present, and capsular process of lower incisor alveoli slightly curved in *O. paricola*, in contrast to short nasal bones, well developed supraorbital ridges that slightly extends onto parietal, mesopterygoid fossa generally extending beyond the maxillary bone, alisphenoid strut always present in at least one side of the skull, anterior opening of the alisphenoid canal always absent, subsquamosal fenestra always absent, and capsular process of lower incisor alveoli moderately curved in *O. auyantepui*.

Oecomys auyantepui is also in sympatry with *Oecomys* sp. B and *Oecomys* sp. C, but it is easily differentiated from the latter two species by the longer (11 mm) and reddish brown dorsal fur, flank lighter and more grayish than dorsum, short nasal bones, supraorbital ridges slightly extending onto parietals, presence of alisphenoid strut, absence of anterior opening of the alisphenoid canal and subsquamosal fenestra, and moderately curved capsular process of lower incisor alveoli (Tables 10 – 11).

Oecomys sp. B and *Oecomys* sp. C are in sympatry in the Guiana center of endemism, and are very closely related according to our molecular analysis. Morphologically, they are very similar to each other, but can be differentiated by the following characters: short tail in *Oecomys* sp. C (about 81 % of head and body length) in contrast to long tail in *Oecomys* sp. B (approximately 120 % of head and body length); central caudal scale hair longer than the lateral ones in the former species, instead of scale hairs similarly long in the latter species; mesopterygoid fossa generally extends beyond the maxillary bone in *Oecomys* sp. C, whereas it never extends beyond the maxillary bone in *Oecomys* sp. B; smaller hindfoot, darker head and body dorsal fur, and the presence of a bright orange line at the limits between dorsal and ventral pelage in *Oecomys* sp. C.

MORPHOMETRIC ANALYSIS

External and cranial dimensions for all *Oecomys* species from eastern Brazilian Amazon are given in Tables 4 – 6, including mean, standard error, ranges and sample size for each variable. Sexual dimorphism was evaluated with Hottelling's T2 test among specimens of *Oecomys paricola* from the Xingu center of endemism (21 males and 17 females), because this was the larger population we examined with balanced proportion between males and females. As the null hypothesis that this population was not sexually dimorphic was rejected

(F=X, p=0.004), we treated *O. paricola* and all other species included in this report as sexually dimorphic in the subsequent multivariate test.

We performed three multiple-groups discriminant analyses based on 16 log transformed cranial variables. The first analysis included all eleven species we recognize for eastern Brazilian Amazon (Figure 6A); the second included only the larger species (*Oecomys catherinae*, *O. rex*, *O.* species B and *O.* species C; Figure 6B); and the third included only the smaller species (*Oecomys auyantepui*, *O. paricola*, *O. bicolor*, *O. cleberi*, *O. rutilus*, *O.* species A and *O.* species D; Figure 6C). Table 11 provides the standardized discriminant coefficients for the first two axes of these analyses. In the analysis including all species, the first axis explained 73.64 % of the total variation and served to separate the four largest species (*O. catherinae*, *O. rex*, *O.* species B, and *O.* species C) from the others (*O. paricola* from *O. cleberi*, *O. rutilus*, *O.* species A and *O.* species D), with the length of lower molar row (LLM) contributing most for discriminating them. The second axis explained 13.99 % of the total variation and served to partially separate *O. cleberi*, *O. rutilus*, *O.* species A, and *O.* species D from *O. auyantepui*, with the length of the palatal bridge (LPB) and the breadth of m1 (Bm1) strongly contributing to discrimination.

In the second analysis, including only the larger species, the first axis explained 64.12 % of the total variation and served to consistently separate *Oecomys rex* from the other three species, and partially separate *O. catherinae* from *O.* species B and *O.* species C. Length of nasals (LN), length of upper molar row (LM), breadth of M1 (BM1) and the braincase breadth (BB) are the variables that strongly contributes to these morphometrical separations. The second axis explained 20.96 % of the total variation and separated *O. rex* from *O. catherinae* and *O.* species B, as well as *O.* species C from *O. catherinae*, with the length of upper molar row (LM), the breadth of M1 (BM1), the occipital condyle breadth (OCB) and the length of lower molar row (LLM) strongly contributing to this result. In the latter analysis, including the remaining species, the first axis explained 58.07 % of the total variation and served to separate *Oecomys auyantepui* and *O. paricola* from *O. cleberi*, *O. rutilus* and *O.* species D, as well as partially separate *O. cleberi* from *O.* species D, with only the length of the palatal bridge (LPB) strongly contributing to this result. The second axis explained 29.87 % of the total variation and barely separated *Oecomys auyantepui* from *O. paricola*, with the breadth of m1 (Bm1) strongly contributing to the result.

Despite the fact that our dataset was not robust and balanced to all species, which may lead to some deviations in this analysis, we conclude that the breadth of the braincase (BB), breadth of m1 (Bm1), breadth of M1 (BM1), length of the lower molar row (LLM), length of the upper molar row (LM), length of nasal (LN), length of the palatal bridge (LPB), and occipital condyle breadth (OCB) are the most relevant measurements to the diagnosis of the species included in this report.

SPECIES ACCOUNTS

According to the literature, only six species of *Oecomys* are expected to occur in the eastern Brazilian Amazon, including the states of Amapá, Pará, and Mato Grosso: *O. auyantepui*, *O. bicolor*, *O. paricola*, *O. roberti*, *O. rex*, and *O. rutilus* (Musser & Carleton 2005; Bonvincino *et al.*, 2008). However, our results showed that this number is largely underestimated; since 11 different forms that effectively represent good species could be recognized by us. Among them, five species are already expected to occur in the region studied (*Oecomys auyantepui*, *O. bicolor*, *O. paricola*, *O. rex*, and *O. rutilus*), and two have never been recorded for the Amazonian region (*Oecomys catherinae*, known to occur in the Atlantic forest, and *O. cleberi*, known only from the type locality in Brazil, Distrito Federal, Universidade de Brasília, Fazenda Água Limpa). In addition, of the 11 species herein recognized, four are either new or not currently recognized taxonomically. They are named *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C, and *Oecomys* sp. D. By contrast, we found no specimens of *Oecomys roberti* among our samples, despite it is expected to occur in the northern part of the state of Mato Grosso.

Bellow, we provide morphological descriptions, brief taxonomic notes, and the complete geographic distribution of each of the 11 species recognized in this report, including maps with collecting localities of specimens herein examined (Figures 7 – 11). For some large sampled species we also provide comments on geographic variation.

Since we did not analyze types associated to *Oecomys*, we chose not to name the forms that are not positively assignable to any of the nominal taxa available. Appropriate description of new forms and or revalidations and re-descriptions of currently synonymized forms will be soon undertaken in another report. In our phylogenetic analysis, we included one unidentified

species which refers to one specimen (MZUSP 29530), but since we have not examined the voucher specimen, we have not included this species in this account.

Oecomys auyantepui Tate, 1939

Geographic distribution: South-central Venezuela eastwards through the Guyana to Amapá, Brazil, and southwards to Amazonas and Pará, Brazil, as far as the left bank of the Amazon River (Musser & Carleton 2005; Figure 7).

Taxonomic notes: Originally described by Tate (1939) based on two adult males and one adult female , adult specimens from southern slopes of Venezuela, Bolívar State, Mt. Auyán-tepui, 1100 m. Tate (1939) presented *O. auyantepui* as a species with gray-based ventral pelage, short feet and slightly tufted tail. The author stated that *O. auyantepui* could be allied to the *trinitatis* group, then related to the genus *Oryzomys*. Based on pelage color similarities, Cabrera (1960) considered it as synonym of *speciosus*. Later, Musser & Carleton (1993) synonymized *auyantepui* under *paricola*, but Voss *et al.* (2001) considered it as a valid species on the basis of cranial morphology and their opinion was followed by Musser & Carleton (2005).

Morphological description: Every comparable character exhibited by specimens that we have identified as *O. auyantepui* matches those features provided in the original description by Tate (1939) and the description of French Guyana specimens by Voss *et al.* (2001), except for the tail color. According to the authors, the tail is uniformly dark brown (almost blackish) tail in the species, but almost all specimens analyzed by us exhibited the ventral side of the proximal part of the tail paler than the distal part of it, being more appropriately defined as slightly bicolored.

Oecomys auyantepui is intermediate in size to other congeneric species (Table 9). The dorsal pelage is smooth, thick and large, reaching 11 mm in length. Head and dorsal pelage vary from yellowish-brown to reddish-brown in adults. Flank is lighter and grayish than dorsum. Ventral pelage is variable in color, being totally gray-based with cream-colored to pale-buff tip, or only laterally gray-based with the pectoral region self-cream or pale; however, chin and throat are always self-colored (cream or pale). The larger mystacial vibrissa is uniformly brown colored; they reach about 40 mm in length, surpassing the ear.

Proportionally to head and body length, the ear length is larger in males than in females and in young specimens, decreasing according to age, ranging from 17 % to 14 % in males and from 15 % to 13 % in females. Skin pigmentation of the ear varies from brown to dark brown. Hairs on external surface of the ears are short but visible without stereomicroscope, with color varying from orange to dark brown, just like dorsal pelage. Internal hairs of ears paler, ranging from cream to orange colored. The tail reaches about 107 % of head and body length, and this is the same proportion in all age classes and sexes. As described above, the tail is slightly bicolored, with the ventral side paler in the proximal part of it. Caudal scales are small, rounded, and arranged in circles. Every caudal scale have three hairs related to it, all three similarly thick, but the central hair is longer than the other, reaching almost three scale rows in length while the others reach only two scale rows. All specimens exhibit a pencil ranging from 5 to 8 mm in length, which is more developed in older than in younger specimens. Body pelage extends maximum 5 mm over the proximal part of the taxidermized tail. Feet reach approximately 19 % of head and body length. *Oecomys auyantepui* exhibit six well developed plantar pads, which is more developed on mature adults. Plantar surface of hands and feet are smooth, but the fingers exhibit dermal folds that remind scales. Claws are curved, and ungual tufts cover only the base of the claws. Roughly, hands and feet color varies from cream to light brown with a brown spot on dorsum that becomes more conspicuous with increasing age.

In general, the skull of *Oecomys auyantepui* has no morphological characters that can be consistently used to discriminate this species from the majority of other species included in this report (Figures 12A and 13A). *O. auyantepui* exhibits short rostrum relative to the skull length; shallow zygomatic notch, which is almost imperceptible dorsally; and divergent interorbital region, just like other congeneric species. Other craniodental characters will be discussed hereafter.

Nasal bone is short, not surpassing the lachrymal-frontal-maxillary suture. Nasal-frontal suture shape varies from squared to moderately V-shaped. Supraorbital ridge is developed, projecting dorsally from the border of the frontal bone at the orbital fossa; it slightly extends onto the parietal bone, and increases in size according to more age. The frontal-parietal suture is usually continuous to the frontal-squamosal suture, although in some specimens the former is posterior to the latter. The parietal broadly extends over the squamosal. Interparietal is well developed, occupying all the braincase width; it is wider than longer, with width larger than the frontal-parietal suture. The anterior edge of mesopterygoid fossa does not reach the

posterior edge of the M3 alveoli, which characterizes a long palate; this edge varies from rounded to W-shaped. Mesopterygoid roof is totally ossified. Incisive foramina vary from oval to teardrop shaped. In general, there is a unique posterolateral pit on each side of the palate, but a small second pit can be present in only one side. Alisphenoid strut often present in both sides of skull, rarely absent in one side. All analyzed specimens have the anterior opening of the alisphenoid canal, and most of them do not have subsquamosal fenestra. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988), in which a large stapedial foramen accommodates the large stapedial artery, the posterior opening of the alisphenoid canal is present, but less conspicuous, and a conspicuous anteroposterior groove on the inner surface of the squamosal and alisphenoid bones usually marks the passage of the supraorbital branch of the stapedial artery along the lateral wall of the braincase. The wall of the internal carotid canal is often composed of only the ectotympanic and the basioccipital bones; however, in some analyzed specimens the periotic reaches the wall of this canal, but its proportion in relation to the ectotympanic and basioccipital bones is not very significant. Mastoid ossification is highly variable, being either totally ossified, with an external groove with or without a dorsal foramen, or partially ossified, with small fenestra on the dorsal margin of the mastoid. The mental foramen opens laterally. Both upper and lower masseteric ridges join only at the anterior end of each ridge, and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli is always present and moderately curved.

There is no accessory labial root on M1. On M1, the anteroflexus is always present (Figure 14 E1). On M2, the protoflexus and an accessory loph posterior to the paracone are always present; in young specimens, the mesoflexus is present as a unique labial fossette on at least one side; in mature adults, the mesoflexus is divided into labial and medial fossetti. The M3 hypoflexus is deep, disappearing only in very old specimens. First and second lower molars (m1 and m2) do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. Anteromedian fossettid is present on m1 (Figure 14 E2). On m3, the posteroflexid is deep, disappearing only in very old specimens.

Oecomys bicolor Tomes, 1860

Geographic distribution: From eastern Panamá to western Colombia and Ecuador, Venezuela, Guyana, Amazonian drainage of Bolivia, Colombia, Peru, Ecuador and Brazil to the Tapajós River (Musser & Carleton 2005; Figure 8).

Taxonomic notes: Described by Tomes (1860) based on a specimen from Ecuador, Morona-Santiago Province, Gualaquiza, Río Gualaquiza, 885 m. *Oecomys bicolor* was treated as a species-group with seven subspecies by Cabrera (1960): *benevolens* Thomas, 1901, *bicolor* Tomes, 1860, *florenciae* J.A. Allen, 1916, *milleri* J.A. Allen, 1916, *nitedulus* Thomas, 1910, *paricola* Thomas, 1904, and *rosilla* Thomas, 1904; and as a species-group with four subspecies by Hershkovitz (1960): *bicolor* Tomes, 1860, *phaeotis* Thomas, 1901, *trabeatus* G.M. Allen & Barbour, 1923, and *occidentalis* Hershkovitz, 1960. Even today, *O. bicolor* is treated as a probable species complex, with 10 junior synonyms: *benevolens* Thomas, 1901; *dryas* Thomas, 1900; *endersi* Goldman, 1933; *florenciae* J.A. Allen, 1916; *milleri* J.A. Allen, 1916; *nitedulus* Thomas, 1910; *occidentalis* Hershkovitz, 1960; *phelpsi* Tate, 1939; *rosilla* Thomas, 1904; and *trabeatus* G.M. Allen & Barbour, 1923 (Musser & Carleton 2005).

Morphological description: Every comparable character exhibited by specimens from Rondônia matches those features of specimens from Juruá River described by Patton *et al.* (2000). However, specimens from Guiana showed some differences that we treated herein as geographic variations.

This species is larger than *Oecomys cleberi*, *O. rutilus* and *Oecomys* sp. D (Table 8). Its dorsal pelage reaches 6 mm in length and is bright brownish orange colored, with head darker and flank lighter than dorsum. Head, dorsum and flank fur are darker in males then in females. Ventral pelage is white to the roots with or without a thin line gray-based at sides. The larger mystacial vibrissa reaches 35 mm in length. The ears are almost naked, brown colored in females and dark brown in males. The tail is brown and slightly bicolored with the ventral side paler in the proximal part of it, about 115 % of head and body length. Caudal scales vary from squared to round shaped and are arranged in circles. The central hair of each scale is longer and thicker than lateral ones, reaching more than two scale rows. All specimens exhibit a short but distinct pencil (< 5 mm in length). Body pelage extends 5 – 8 mm over the proximal part of the taxidermyzed tail. Feet are broad and reach approximately 15 % of head and body length. Plantar surface exhibit a few *squamae* and dermal folds in

fingers, as well as six much developed plantar pads. Claws are curved, and ungual tufts cover only the base of the claws. The dorsal surface of feet and hands are covered mainly with pure brown and brown-based hairs, which leads to a conspicuous spot on metatarsals.

The skull of *Oecomys bicolor* is longer and narrower than other morphologically closed species (*O. cleberi*, *O. rutilus* and *Oecomys* sp. D), except by *Oecomys* species A (Figures 12B and 13B). The nasal-frontal suture is squared, continuous to pre-maxillary-frontal suture. Supraorbital ridge is slightly developed, projecting dorsally from the border of the frontal bone at the orbital fossa; it slightly extends onto the parietal bone. The frontal-parietal suture is usually continuous to the frontal-squamosal suture. The parietal broadly extend over the squamosal. Interparietal is very short in length but wide, with the interparietal-parietals suture at the same length of frontal-parietals suture. The zygomatic plate is thin and short. The anterior edge of mesopterygoid fossa does not reach the posterior edge of the M3 alveoli; this edge varies from square to round shaped. Mesopterygoid roof is totally ossified. Generally, there is one large posterolateral pit on each side of the palate. Incisive foramina are teardrop shaped, at the same length or shorter than palatal bridge. Alisphenoid strut is always absent. The anterior opening of the alisphenoid canal is present. The subsquamosal fenestra varies from very small, when the subsquamosal process is thick and short, to largely opened, when the subsquamosal process is thin and long. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal is often composed of only the ectotympanic and the basioccipital bones; however, in some analyzed specimens the periotic reaches the wall of this canal, but its proportion in relation to the ectotympanic and basioccipital bones is not very significant. Mastoid ossification varies from totally ossified to the presence of a foramen on the dorsal margin of the mastoid. The mental foramen opens laterally. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli is always present but slightly curved.

An accessory labial root is always present in M1. The anteroflexus is also present on M1 as a single internal fossette (Figure 14 G1). On M2, the protoflexus is absent, but an accessory loph posterior to paracone is present; the mesoflexus is a single internal fossette. Hypoflexus is always present on M1 but is shallow. There is an accessory labial root on m1. The anteromedian fossettid is present on m1 (Figure 14 G2). On m3, the posteroflexid is deep.

Geographic variation: Specimens from Guiana are smaller, darker and more yellow-grayish than specimens from Rondônia and Juruá River. The specimens from Guiana also have the tail similar in size with the head and body length, the alisphenoid strut always present on at least one side of the skull, the nasal-frontal suture more rounded, and the interparietal longer and wider.

Oecomys catherinae Thomas, 1909

Geographic distribution: Forested zones in Brazil south of the Amazon River, from the Madeira River to the Tocantins River, and in the Atlantic Forest from the state of Paraiba southwards to the state of Santa Catarina, including part of the states of Minas Gerais and Goiás (Musser & Carleton 2005; Bonvincino *et al.* 2008; Figure 9).

Taxonomic notes: *Oecomys catherinae* was described by Thomas (1909) synonymized under *Oryzomys subflavus* Wagner, 1842 by Hershkovitz (1960) but considered as a valid species by Cabrera (1960). Hershkovitz (1960) described *Oryzomys bahiensis*, a replacement for *Mus cinnamomeus* Pictet & Pictet, 1844 preoccupied by a *Proechimys* species. However, both nominal taxa are currently considered junior synonyms of *Oecomys catherinae*, which in turn is treated as a valid species of the *Oecomys trinitatis* group in the taxonomic compendium of Musser & Carleton (2005).

Morphological description: Since the holotype of this species was described on the basis of specimens from Joinville, Santa Catarina, Brazil, in the Atlantic Forest, we considered some differences in specimens from the Amazon Forest as geographic variations. In general, all specimens analyzed by us match the original description by Thomas (1909).

Oecomys catherinae is the largest species analyzed by us (Table 9). Its fur is soft and thick, reaching 13 mm in length at dorsum. Head and body pelage is yellow-grayish. Flank is slightly lighter than dorsum. Ventral pelage is totally gray-based and white-tipped, with a pure white spot in throat. The larger mystacial vibrissa reache about 45 mm in length, surpassing the ears. This latter is short, about 14 % of dead and body length, brown colored, lighter inside than outside. The tail is dark brown with the ventral proximal part lighter, about 123 % of head and body length, with rounded scales arranged diagonally. All three scale hairs are similarly thick, but the central hair is slightly longer than lateral hairs, reaching two scales

rows in length. There no conspicuous caudal tuft. Body pelage extends maximum 10 mm over tail. Feet are short and broad, about 22 % of head and body length, with six plantar pads well developed. Feet and hands are pure white colored with a brownish spot on metatarsals, with *squamae* in plantar surface and dermal fold in fingers. Claws are curved with white ungual tufts longer than claws.

Oecomys catherinae has a large, narrow and flat skull with short rostrum (Figures 12C and 13C). The nasal-frontal suture varies from squared to slight rounded and is continuous to pre-maxillary-frontal suture. Supraorbital ridges are well developed, passing back as strongly marked ridges across the parietals. The zygomatic plate is broad with small projection of the anterior edge, turning the zygomatic notch notable at dorsal view. Frontal-parietal and frontal-squamosal sutures are continuous. The parietal bones are slightly expanded below the lateral surface of the braincase. Interparietal bone is rounded, almost longer than broader with the parietals-interparietal suture at the same size or about 1 mm smaller than frontal-parietals suture. There is one or two large posterolateral pits on palate. Incisive foramina are longer and narrow. Mesopterygoid fossa is broad with the anterior edge slightly rounded not surpassing the posterior edge of the maxillary bone, and its roof totally ossified. Subsquamosal process is very short and broad, which leads to a small subsquamosal fenestra. Alisphenoid strut is always absent at both sides, but the anterior opening of the alisphenoid canal is large and always present at both sides. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The only skull we analyzed from the Atlantic Forest do not exhibit the bullae, ossicles and associated foramina, but in all other specimens the wall of the internal carotid canal composed always only by the bullae and the basioccipital and the mastoid ossification varying from totally ossified to the presence of a small fenestra. The mental foramen opens frontally. Both lower and upper masseteric ridges conjoined as a single crest under m1 alveoli. The capsular process of lower incisor alveoli is always present and well developed.

An accessory labial root is always present in M1. The anteroflexus is also present as a single internal fossette on M1 (Figure 14 D1). The protoflexus is absent on M2, but the accessory loph posterior to paracone is present. The mesoflexus on M2 is a single internal fossette. The hypoflexus is always present on M3 but is shallow. On m1, there is an accessory labial root. A shallow anteromedian fossettid is also present on m1 (Figure 14 D2). The posteroflexid is always present and deep on m3.

Geographic variation: In some specimens from the Xingú and Rondônia centers of endemism, the subsquamosal fenestra is absent. Specimens from Xingú region show the lower masseteric ridge more conspicuous than the upper masseteric ridge. The specimen MPEG39904 is dark reddish colored in head and dorsum pelage, and the specimen MPEG38898 showed the interparietal bone more like *O. auyantepui*, i.e. much broader than larger, with the parietals-interparietal suture larger than frontal-parietals suture. Specimens from the Rondônia region show smaller feet and tail than specimens from other regions. The specimen MPEG12656 show the frontal-parietal suture posterior to the frontal-squamosal suture, and the parietals restrict to the dorsal surface of the braincase. Finally, the specimen MPEG34224 show alisphenoid strut at one side of skull.

Oecomys cleberi Locks, 1981

Geographic distribution: Brazil, south of the Amazon River, between the rivers Xingú and Tocantins, southward to its type locality in Brazilian Federal District (Figure 8).

Taxonomic notes: Described by Locks (1981) based on an adult female. *O cleberi* has been morphologically associated to *Oecomys bicolor* (Tomes, 1860) and *O. milleri* J.A. Allen, 1916, the latter of which is currently considered a junior synonym of *O. bicolor*. **Morphological description**: This species is about the same size of *Oecomys rutilus* (Table 8). Old specimens are yellowish-brown at head and dorsum. Flank is lighter than dorsum with a bright yellow line at the limits to ventral surface. Ventral fur varies from pure white to light gray-based, but chin and throat are always white to the roots. Young adults are darker than old ones in head, dorsum and flank pelage; however, one mature adult shows sparsely pelage, more grayish, like a young specimen. The larger mystacial vibrissa reaches 35 mm in length. Ears are short, approximately 14 % of head and body length, and light brown colored in old specimens and dark brown in young adults. Dorsal fur is short, about 5.5 mm in length. Tail is about the same size of head and body (101 %), dark brown with small squared scales arranged in circles. Every caudal scale have three hairs related to it, all three similarly thick, but the central hair is longer than the other; males showed this hairs very longer, central hairs reach three scales while lateral hairs reaches two scales in length; females showed shorter hairs than males, with central hair reaching no more than two scales while lateral ones a little more than one scale in length. There is a small pencil reaching from 3 to 4.5 mm in length. Body pelage

extends from 5 to 10 mm over the proximal part of tail. Feet are small and narrow, approximately 21 % of head and body length, with six plantar pads well developed and a few *squamae* at the central part of plantar surface. Claws are curved with white ungual tufts covering an half of each claw. Fingers are mainly covered by pure white hairs, however there some brown-based hairs next to metatarsals. Dorsum of feet and hands are uniformly covered by pure white, pure brown and brown based hairs, which leads to cream colored dorsum; one specimen (MG39785) showed a conspicuous dark brown spot on metatarsals.

Oecomys cleberi skull is about the same size and shape of *Oecomys rutilus* skull (Figures 12D and 13D). The rostrum is short with a nasal-frontal suture squared to V-shaped generally continuous with pre-maxillary-frontal suture. Supraorbital ridge is present but slightly developed. Zygomatic plate is thin without projection of its anterior edge. Frontal-parietal and frontal-squamosal sutures are continuous. Parietals broadly extending onto lateral surface of the braincase. Interparietal with interparietal-supraoccipital suture moderately rounded, wider than longer, but smaller than the posterior part of the braincase in breadth and length, with frontal-parietal and parietal-interparietal sutures ate the same size. Generally, there is one large posterolateral pit on each side of the palate. Incisive foramina is narrow and about the same length than palatal bridge. Mesopterygoid fossa open U-shaped, do not extending beyond the posterior border of the maxillary bone and with its roof totally ossified. Alisphenoid strut is always absent and the anterior opening of the alisphenoid canal is always present. The subsquamosal process is very thin and longer and the subsquamosal fenestra is always moderate in size. This species showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). Generally, the wall of the internal carotid canal composed only by the bullae and the basioccipital bones; however the periotic can compose this wall too. The mastoid ossification varies from totally ossified to the presence of a small fenestra on top. The mental foramen opens laterally. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli present but slightly curved.

An accessory labial root present in M1. On M1, the anteroflexus is always present as a single internal fossette (Figure 14 I1). Protoflexus is absent on M2, and the presence of an accessory loph posterior to paracone is variable. Mesoflexus on M2 is a single internal fossette. Hypoflexus always present on M3 but shallow on young adults; in old specimens it is absent or present as a very small and shallow depression. On m1 and m2 there is no accessory

roots or divisions of the anterior root, thus this molar presents only two roots. Anteromedian fossettid is present on m1 (Figure 14 I2). Posteroflexid is present and deep on m3.

Oecomys paricola (Thomas, 1904)

Geographic distribution: Brazil, south of the Amazon River, from the right margin of the Xingu River to the eastern border of the state of Pará, including the Marajó Island (Figure 7).

Taxonomic notes: This species was described by Thomas (1904) under the genus *Rhipidomys* as a very small species of the *Rhipidomys dryas* group. Thomas (1906) synonymized *R. dryas* Thomas, 1900 under *Oecomys bicolor* (Tomes, 1860) when he described this genus. The type of *O. paricola* is a female specimen from Igarapé-Assú, Pará State, Brazil. Thomas (1904), considered it closely allied to *R. dryas*, from which it can be readily differentiated by its much duller coloration and its smaller skull size. Cabrera (1960) considered it as a subspecies of *Oryzomys (Oecomys) bicolor*, disagreeing with Hershkovitz (1960) who synonymized it under *Oryzomys (Oecomys) bicolor*, and considered skull size and coat color of *paricola* as morphological variations of *bicolor*. Musser & Carleton (1993) recognized *Oecomys paricola* as a valid species and also included *O. auyantepui* Tate, 1939 as its junior synonym. However, *O. auyantepui* was revalidated by Voss *et al.* (2001), an opinion followed by subsequent authors.

Morphological description: The morphological features of *O. paricola* described in this report were based mainly on specimens from the east margin of the Tocantins River, the same region of its type locality. Different morphotypes of other populations were assumed to be geographic variants and are described further in this species account. Specimens from the Belém center of endemism are identical to the ones reported in the species original description (Thomas 1904), and to those used by Voss *et al.* (2001) for comparisons with *O. auyantepui*.

Oecomys paricola is smaller than *O. auyantepui* (Table 9). The dorsal pelage is smooth and reaches about 9 mm in adults. Head and dorsum fur are dark yellowish-brown. Flank is lighter than dorsum. Ventral surface are totally grey-based with white tip, but chin and throat are white to the roots. Mystacial vibrissae are blackish with uncolored tip, reaching 40 mm in old specimens. Ear is short, approximately 14 % of head and body length, with dark brown hairs outside and dark orange hairs inside. The tail reach about 112 % of head and body

length and is dark brown slightly bicolored, with the ventral side paler in the proximal part of it. Scales are small and rounded arranged in circles. The three scale hairs are similarly thick with the central hair longer than lateral ones, reaching almost three scales in length in contrast to the lateral hairs that reaches two scales. There is always a distinct pencil reaching 6.5 mm in old specimens. Body pelage extends maximum 10 mm over the taxidermyzed tail. Feet are short and narrow, reaching 21 % of head and body length, with six plantar pads well developed. Feet and hands has smooth plantar surface with dermal folds on fingers. Dorsal surface varies from cream to lighter brown with a brown spot on metatarsals, with hairs totally cream colored and totally dark brown, besides brown-based and cream tip hairs. Claws are curved and ungual tufts cover only the base of the claw.

This species has a narrow and delicate skull (Figures 12E and 13E). Nasal bone is long, surpassing the pre-maxillary-frontal suture, with the nasal-frontal suture generally slightly rounded. Supraorbital ridge is slightly developed. Zygomatic plate does not show any projection of its anterior edge. Frontal-parietals and frontal-squamosal sutures are continuous. Parietals broadly extend onto lateral surface of braincase. Interparietal is well developed, occupying all the braincase breadth, it is wider than longer, and its breadth is larger than the frontal-parietal suture. Generally, there is one large posterolateral pit on each side of the palate, however a few specimens showed two or three smaller pits at least on one side. Incisive foramina are oval-shaped. The mesopterygoid fossa anterior edge varies from squared to moderate rounded shaped and never pass the posterior edge of the maxillary bone. Mesopterygoid fossa roof is totally ossified. Alisphenoid strut is always absent. The subsquamosal fenestra and the anterior opening of alisphenoid canal are always present. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal is composed often only by the bullae and the basioccipital bones, however in some analyzed specimens the periotic reaches the wall of this canal, but its proportion in relation to the bullae and basioccipital is no very significant. Mastoid bone often shows a large foramen on top, but a few specimens exhibit this foramen very small. The mandible is delicate, like the skull, with a mental foramen laterally disposed. Both upper and lower masseteric ridges join only on anterior tip of each ridge and don’t pass the m1 alveoli. The capsular process of the lower incisor alveoli is slightly curved.

There is no accessory labial root in M1. Anteroflexus is also present as a single internal fossette (Figure 14 F1). Protoflexus and an accessory loph posterior to paracone are present on M2. Mesoflexus on M2 is a single internal fossette in young specimens, but is divided into

labial and medial fossetti at least on one side of adults. Hypoflexus is present on M3 but is shallow. On m1 and m2 there is no accessory roots or divisions of the anterior root, thus this molar presents only two roots. Posteroflexid is always present and deep on m3 (Figure 14 F2).

Geographic variation: All specimens from the Marajó Island and a few specimens from the Xingú region are greater in size than specimens from the Belém region, resembling *O. auyantepui* in exhibiting well developed supraorbital ridges. Specimens from the Marajó Island and Xingú region are also distinct in having tail scales more rounded, with longer hairs than the specimens from Belém, darker feet with a conspicuous dorsal spot in old individuals, plantar surface of feet with *squamae* in a few specimens, generally the nasal bone short, without passing back the pre-maxillary-frontal suture, markedly rounded nasal-frontal suture, variable positions between frontal-parietal and frontal-squamosal sutures, anterior edge of mesopterygoid fossa generally surpassing the posterior edge of the maxillary bone but never reaching M3 alveoli, presence or absence of the subsquamosal fenestra, anterior opening of the alisphenoid canal very variable, generally the mastoid bone totally ossified, and well developed mesoloph in m3. Specimens from the Marajó Island also resemble *O. auyantepui* in exhibiting a conspicuous midline of self-white hairs on ventral pelage, and robust mandible with conspicuous capsular process of lower incisor alveoli.

Oecomys rex Thomas, 1910

Geographic distribution: Eastern Venezuela eastwards through the Guyana to Amapá, Brazil, as far as the north margin of the Amazon River (Figure 9).

Taxonomic notes: Described by Thomas (1910) as a large species of *Oecomys* with much developed supraorbital ridges and general appearance of *O. catherinae* Thomas, 1909. Cabrera (1960) considered it as a subspecies of *O. catherinae*, but Hershkovitz (1960) treated both taxa as subspecies of *Oryzomys subflavus* Wagner. In the same work, Hershkovitz (1960) changed *Oecomys rex* name to *O. regalis* (Hershkovitz, 1960), because the homonymy with *Calomys rex* Winge recognized as *Oryzomys* at that moment. Musser & Carleton (1993) recognized it as a valid species of *Oecomys*, an opinion followed by subsequent authors.

Morphological description: This species is easily identified by its short and broad skull with a conspicuous postorbital process, but a young specimen examined (IEPA2410) does not

show this process. The only difference we found between our morphological data and the description of French Guyana specimens provided by Voss *et al.* (2001) was the alisphenoid strut absent in our specimens, compared to the presence or absence in those specimens. However, since our sample is much reduced, we do not consider this character as discrepant. Comparing our data to the original description (Thomas, 1910), we found that every comparable character matches.

This species is smaller than its sister-species *Oecomys catherinae*, but it is intermediate to large in size compared to other congener species (Table 9). *Oecomys rex* is dark yellow-grayish at dorsum. Flank is lighter than dorsum. Ventral pelage is totally dark gray-based and white-tipped with a small pure white spot on throat. Dorsal pelage is smooth and long, reaching more or less than 13 mm in length. The dark-brown, almost blackish, tail is about 115 % of head and body length with rounded scales arranged in circles and no pencil on tip. The central hair of each scale is thicker and longer than lateral ones, reaching almost two scale rows; young specimens showed more squared scales with all hairs at the same length (almost two scales). Body pelage extends 4 – 5 mm over tail. Feet are larger and broad, about 18 % of head and body length. All six plantar pads are well developed and the plantar surface of hands and feet are covered with *squamae* and dermal folds in fingers. Claws are curved and reach 1 mm in hands and 2 mm in feet, with ungual tufts pure white covering all claw bases and more than a half of the claw in length. Dorsum of feet and fingers are totally covered with dark brown based and white-tipped hairs, however, the general coloration of it varies from cream to light brown, with no darker spot. Feet skin of young specimen is mainly whitish with more totally blackish and black-based hairs, and the ungual tuft is black-based totally covering the claw in length.

Oecomys rex has a short and broad skull with braincase and rostrum convexes forming a notable depression in the beginning of the inter-orbital region (Figures 12F and 13F). Nasal bone is short, with nasal-frontal suture slight rounded and anterior to pre-maxillary-frontal suture. Supraorbital ridges strongly diverge and are well developed even in young specimens, but are much developed in old ones. After the supraorbital ridge there is a conspicuous postorbital horizontal process, which is an important character for the recognition of this species. There is a slightly development of the anterior edge of the zygomatic plate. Frontal-squamosal suture is continuous to frontal-parietal suture. Parietal bone broadly extends upon squamosal bone. Interparietal bone is well developed, wider than longer, occupying all the braincase breadth. There is one posterolateral pit at each side of the palate, but small second

pit can appear in one side of palate. Incisive foramina are large and oval-shaped. The sphenopalatines vacuities are present but reduced as narrow openings situated before and after basisphenoid-presphenoid suture. Mesopterygoid fossa anterior edge varies from squared to accentuate rounded. Subsquamosal process is very short and broad, which leads to a small subsquamosal fenestra. Alisphenoid strut is always absent at both sides, but the anterior opening of the alisphenoid canal is large and always present at both sides. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal is composed always only by the bullae and the basioccipital bones. The mastoid bone is totally ossified. The mental foramen opens frontally, like in *Oecomys catherinae*. The lower masseteric ridge is more conspicuous than upper ridge, but both ridges conjoined as a single crest under m1 hypoconule and stay as a unique ridge to anterior edge of m1 alveoli. The capsular process of lower incisor alveoli is always present, but reduced to a slight rounded elevation.

There is no accessory labial root at M1. Anteromedian flexus is generally absent on M1 (Figure 14 A1); however the young specimen shows it. Anteroflexus is also present as a single labial fossette on young and young adult specimens but divided into labial and medial fossetti in mature and old adults. Protoflexus is absent on M2, but an accessory loph posterior to paracone is present. Mesoflexus on M2 is a single internal fossette. Hypoflexus is also present on M3, but is shallow. First and second lower molars do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. Anteromendian fossettid is always present on m1 (Figure 14 A2). Posteroflexid is present and deep on m3.

Oecomys rutilus Anthony, 1921

Geographic distribution: From extreme eastern Venezuela eastwards through the Guyana to Amapá, Brazil, and southwards to Amazonas and Pará, Brazil, north of the Amazon River (Figure 10).

Taxonomic notes: *Oecomys rutilus* was described by Anthony (1921) as a small, brightly colored species with very short tail and clear white underparts, based on an adult female from Guyana, Mazaruni-Potaro District, Kartabo. The author pointed out that the species might be associated with *rosilla* Thomas, 1904, but differed from it by the smaller size and underparts white instead of ochraceous. Cabrera (1960) treated it as a junior synonym of *Oryzomys*

(Oecomys) bicolor nitedulus (Thomas, 1910), considering the type of *rutilus* as an individual or population variant of *nitedulus*. At the same time, Hershkovitz (1960) considered *rutilus* as a junior synonym of *Oryzomys (Oecomys) bicolor bicolor* (Tomes, 1860), based only on the original description, without examining the type of *O. rutilus*, which he believed was a subadult of the *nitedulus* series described by Anthony from the same place. Voss *et al*. (2001) formally differentiated *O. rutilus* from *O. bicolor* based on morphological and morphometric characters, revalidating it. Their opinion has been followed by subsequent authors.

Morphological description: *Oecomys rutilus* is small in size compared to other congeneric species (Table 8). The dorsal fur is smooth, thick and large, reaching 8 mm in old specimens. Head and dorsal pelage varies from yellowish-brown to reddish-brown in adults. Flank is lighter and grayish than dorsum, like in *O. auyantepui*. Ventral pelage is white to the roots with a thin line of gray-based hair in limits with flank. Adult females are smaller and more grayish than males of the same age, and also showed pelage softer like young individuals. The mystacial vibrissa reaches 40 mm in length and is blackish with white tip. Ears are larger, approximately 16 % of head and body length, and have the border dark brownish and the base cream colored. The tail reach about 114 % of head and body length and are uniformly brown colored, ranging from dark brown in young specimens and light brown in old ones. Scales are rounded arranged in circles, with the central hair longer and thicker than lateral ones, reaching almost three scale rows in length. There is a conspicuous pencil that reaches 9 mm in length. Body pelage extends maximum 8 mm over proximal portion of taxidermyzed tail. Feet are narrow and long, about 23 % of head and body length. The plantar surface is generally smooth, but some specimens showed a few *squamae* on it. There are six plantar pads well developed, however smaller than in *O. bicolor*. Claws are curved and covered by larger ungual tufts that cover almost all claw in length. Dorsal surface of feet and hands are covered with pure white and pure dark brown hairs with a high density of dark brown hairs next to the finger bases, which leads to a diffused spot on metatarsals.

The skull of *O. rutilus* is small and inflated (Figures 12G and 13G); female skulls are also smaller and more inflated than male skulls. Nasal bone is short, never surpassing the pre-maxillary-frontal suture, with accentuated rounded nasal-frontal suture. Supraorbital ridge is slightly developed, restricted to frontal bone. The anterior edge of the zygomatic plate does not show projection. The squamosal process of the zygomatic is substantially short and the jugal bone much developed. The frontal-squamosal suture can be continuous or anterior to frontal-parietal suture. Parietals broadly extend upon squamosal. Interparietal is well

developed, occupying all the braincase width, is wider than longer, its breadth is about the same as the frontal-parietal suture. Generally, there is one small posterolateral pit on each side of the palate. Incisive foramina are teardrop-shaped. The mesopterygoid fossa has a totally ossified roof and its anterior edge squared or slightly rounded shaped never extending beyond M3 alveoli. Alisphenoid strut is generally present on both sides and the anterior opening of the alisphenoid canal is always present but small. The subsquamosal process is thin and longer and the subsquamosal fenestra is always present and large. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal is composed often by the periotic together with bullae and basioccipital bones, however in some specimens this canal wall is composed only by these last two bones. Mastoid bone generally shows a small fenestra on top of the bone. The mental foramen opens laterally. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli is always present and moderately curved.

There is an accessory labial root on M1. On M1, the anteroflexus is present (Figure 14 J1). On M2 the protoflexus and an accessory loph posterior to paracone are always present. The mesoflexus is always present as a unique internal fossette on M2. The M3 hypoflexus is deep. First and second lower molars (m1 and m2) do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. The anteromedian fossettid is present on m1 (Figure 14 J2). On m3, the posteroflexid is deep.

Oecomys species A

Geographic distribution: Brazil, between the rivers Madeira and Tapajós (Figure 8).

Morphological description: Morphologically, this species is similar to *Oecomys bicolor* and *O. rutilus*, with which they share a completely pure white ventral surface and a small and delicate skull. We tried to associate the species with one of the ten synonyms currently recognized for *O. bicolor* based on the original descriptions, but none seem to fits it. Evidently, the types of these nominal taxa still need to be examined in order to name the species appropriately.

Oecomys species A is about the same size of *O. bicolor* (Table 10) with smooth intermediate pelage in length, about 10 mm. Dorsal fur is dark reddish with the back parts bright reddish. Head is more dark brown than dorsum. Flank is lighter and brighter than head and dorsum with back parts bright orange and anterior parts and the lateral side of head bright yellowish. Ventral surface is white to the roots with inner part of legs light gray-based. The large mystacial vibrissa reaches 40 mm. Ear is dark brown, lighter inside, reaching 17 % of head and body length. The tail is densely haired with hairs white and black colored, giving a griseous aspect to it. Scales are squared and arranged in circles, with the central hair longer than lateral ones, reaching almost three scales in length contrasted to two scales reached by the lateral hairs. The pencil reaches 9 mm in length. Body pelage extends about 4 mm over the taxidermyzed tail. Feet are large and narrow, approximately 23 % of head and body length. Plantar surface of feet and hands are smooth with six pads well developed. Claws are curved with ungual tuft covering almost all of it in length. Dorsum of feet, hands, fingers and ungual tuft are covered by white, brown and brown-based hairs, with more brown hairs in metatarsals, forming a distinct dark spot.

The skull is rounded like in typical small species of *Oecomys* (Figures 12H and 13H). Nasal bone is long, surpassing the pre-maxillary-frontal suture, with rounded nasal-frontal suture. Supraorbital ridge is slightly vertical developed, restricted to frontal bone. The anterior edge of the zygomatic plate does not show projection. Frontal-parietal suture is continuous to frontal-squamosal suture. Parietals broadly extend onto lateral surface of the braincase. Interparietal is wider than longer, with parietals-interparietal suture about the same size of frontal-parietals bones. The palatal bridge exhibits two small posterolateral pits. Incisive foramina are large. The anterior edge of the mesopterygoid fossa is rounded and extends beyond the posterior edge of the maxillary bone, but do not reaches the M3 alveoli. Mesopterygoid fossa roof is totally ossified. Alisphenoid strut present at both sides of skull. The anterior opening of the alisphenoid canal is present at both sides but small in size. Subsquamosal process is longer and thin and the subsquamosal fenestra is large. The specimen showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal is composed only by the bullae and the basioccipital bones. Mastoid is totally ossified. The mental foramen is positioned more in the diastema than in the lateral surface of the mandible. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli well developed.

There no accessory labial root on M1. The anteroflexus is present (Figure 14 H1). On M2 the protoflexus is present; there is no accessory loph posterior to paracone. Mesoflexus on M2 is a unique internal fossette. Hypoflexus in M3 is present but very small. First and second lower molars (m1 and m2) do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. There is an anteromedian fossettid on m1 (Figure 14 H2). Posteroflexid is present in m3.

Oecomys species B

Geographic distribution: The Amazon and Tocantins River basins in Brazil including the states of Amazonas, Amapá, Pará, Mato Grosso, and Tocantins (Figure 11).

Morphological description: In a first analysis of morphological characters, we considered the specimens of *Oecomys* sp. B as a geographical variation of *O. trinitatis*. In fact, they are morphologically similar to *O. trinitatis* and *O. roberti*, but we were not able to consistently associate them to any one of these species on the basis of original descriptions (J.A. Allen & Chapman 1893; Thomas 1904) and Patton *et al*.'s (2000) description of specimens from the Juruá River. As discussed before, *Oecomys* sp. B also constitutes a monophyletic group which is statistically well supported and exhibit high levels of cytochrome-*b* nucleotide divergences when compared to *O. trinitatis* (12 %) and *O. roberti* (7 %). Genetically, the species is closely related to *O. roberti* from Juruá, but less similar to that regarding morphological features. Since *O. roberti* and *O. trinitatis* have a large number of nominal taxa associated with them, and we did not examine types, we preferred to treat the species as *Oecomys* species B.

This species is a medium to large-bodied *Oecomys* (Table 10) with long tail, approximately 120 % of head and body length, and smooth pelage ranging in length from 6 – 9 mm with no age variation. Head and dorsal pelage varies from grayish-yellow to grayish-brown. Flank lighter than dorsum, but not well marked like in *Oecomys auyantepui*. Ventral pelage is totally gray-based and white-tipped with chin and throat always pure white. Specimens collected a long time ago are generally more yellowish. The larger mystacial vibrissa reaches about 42 mm in length, surpassing the ear, and it is uniformly dark brown colored. Proportionally to head and body, the ear is intermediate in size, about 13 %, and dark brown colored with dark brown hairs outside and light brown hairs inside ears. Tail is dark brown colored, with proximal ventral hairs brown. There no pencil. Scales are squared to

round shaped and arranged in circles, with the central hair slightly longer than lateral hairs, but both reach almost two scales in length. Body pelage extends maximum 10 mm over proximal portion of taxidermyzed tail. Feet are larger and broad, about 22 % of head and body length. All six plantar pads are well developed, but less than in *Oecomys auyantepui*. Plantar surface of hands and feet are smooth, but the fingers exhibit dermal folds. Claws are curved reaching 1 mm in hands and 2 mm in feet, with ungual tufts covering the base of the claws. Dorsum of feet and fingers are totally covered with dark brown based and white-tipped hairs, however, the general coloration of it varies from cream to light brown; there is no darker spot on feet dorsum.

Oecomys species B exhibits a very robust, narrow and flat skull(Figures 12I and 13I). The nasal bone is usually long, surpassing the lachrymal-frontal-maxillary suture, but it may be continuous; nasal-frontal suture shape varies from squared to rounded. Supraorbital ridge is conspicuous and develops vertically. Generally, frontal-squamosal suture is anterior to frontal-parietal suture. Parietal bone broadly extends upon squamosal bone. Interparietal is well developed, wider than longer, but narrower than braincase. The palatal bridge usually exhibits one large posterolateral pit on each side, however some specimens two or three smaller pits. Incisive foramina are teardrop-shaped. The anterior edge of mesopterygoid fossa does not reach the posterior edge of maxillary bone and is variable in shape. Mesopterygoid roof is totally ossified. Alisphenoid strut always absent in both sides. The anterior opening of the alisphenoid canal is always present, but small. Subsquamosal fenestra is always present. All specimens showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal composed often only by the bullae and the basioccipital bones, however in some analyzed specimens the periotic reaches the wall of this canal, however its proportion in relation to other bones is trivial. Mastoid can be totally ossified, or with superior foramen, or with small fenestra on top of the bone. The mental foramen opens laterally, but one specimen (IEPA1535) presented an accessory mental foramen on the right side of the mandible. Both upper and lower masseteric ridges join only on anterior tip of each ridge and don’t surpass the m1 alveoli. The capsular process of the lower incisor alveoli is always present, but slightly curved.

There is no accessory labial root on M1. On M1, the anteroflexus is always present (Figure 14 C1). On M2 the protoflexus and an accessory loph posterior to paracone are always present. Generally, mesoflexus on M2 is a unique labial fossette, but sometimes it could appear divided into labial and medial fossetti on at least one side. Hypoflexus in M3

always present in age 2, but in some specimens from age 3 it is absent or very small and shallow. First and second lower molars (m1 and m2) do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. On m1, the anteromedian fossettid is present (Figure 14 C2). Posteroflexid present in m3, but absent or reduced to a small enamel island on old specimens.

Geographic variation: Specimens from Belém and Xingu are smaller than those from Guiana, especially in skull size. We also noted that posterolateral pits in palate are significantly smaller in specimens from Belém and Xingu compared to the specimens from Guiana, but this feature may be related to the skull size. Individuals from Xingu exhibit darker grayish pelage than those from Belém and Guiana.

Oecomys species C

Geographic distribution: The Amazon River basin to the south of the Amazon River in Brazil, including the states of Amazonas, Pará, and Mato Grosso (Figure 10).

Morphological description: We first grouped these specimens as *Oecomys trinitatis*, but after the molecular analysis we were able to recognize them as a distinct species. Roughly, *Oecomys* sp. C is very much similar to *O.* species B, but a few cranial and external characters can be used to separate them, as discussed in the Morphological Analysis section.

We analyzed the morphology of one young adult male (IEPA2445) that retained juvenile external characters. This specimen is intermediate in size compared to other congener species (Table 10), with short tail, approximately 81 % of head and body length, and smooth long pelage (9 mm in length). Head and dorsal pelage is yellowish dark brown colored. Flank is lighter than dorsum with a line almost bright orange abruptly marking the transition between dorsum and venter. Ventral surface is totally gray-based with chin and throat pure white; inside legs and pectoral parts are lighter grayish than other ventral parts. The larger mystacial vibrissa is dark brown and reaches 35 mm in length, surpassing the ear. Ear is 15 % of head and body length, dark brown outside and light brown inside. Tail is brown with squared scales arranged in circles, and the central hair one scale row larger than lateral hairs. It was impossible to determine presence or absence of pencil since it is broken on tip. Body pelage extends 5 mm over proximal portion of taxidermyzed tail. Feet are short and narrower

than *Oecomys* sp. B, about 16 % of head and body length. All six plantar pads are developed like in *Oecomys* sp. B. Plantar surface of hands and feet are smooth, but the fingers exhibit dermal folds. Claws are curved and reaches 1 mm in hands and 1.5 mm in feet. Ungual tufts cover the base of the claws. Dorsum of feet and fingers are totally covered with dark brown based and white-tipped hairs, however, the general coloration of it varies from cream to light brown; there is no darker spot on feet dorsum.

Oecomys sp. C has a robust, narrow and flat skull (Figures 12J and 13J). Nasal bone is long with nasal-frontal suture V-shaped, surpassing the lachrymal-frontal-maxillary suture. Supraorbital ridge is conspicuous and develops vertically. Frontal-squamosal suture is anterior to frontal-parietal suture. Parietal bone broadly extends upon squamosal bone. Interparietal is well developed, wider than longer, but is shorter in breadth than braincase breadth. The palatal bridge exhibits two posterolateral pits on each side. Incisive foramina are drop-shaped. The anterior edge of mesopterygoid fossa surpasses the posterior edge of maxillary bone, reaching M3 alveoli, and is variable in shape. Mesopterygoid roof is totally ossified. Alisphenoid strut is absent in both sides. The anterior opening of the alisphenoid canal is present but small. Subsquamosal fenestra is present. This species showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). The wall of the internal carotid canal composed only by the bullae and the basioccipital bones. The mastoid bone has a small foramen on top. The mental foramen opens laterally. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do not surpass the m1 alveoli. The capsular process of the lower incisor alveoli is present but slightly curved.

There no accessory labial root on M1 and the anteroflexus is present (Figure 14-B1). On M2 the protoflexus and an accessory loph posterior to paracone are present. Mesoflexus on M2 is a unique labial fossette. Hypoflexus in M3 is present. First and second lower molars (m1 and m2) do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots. On m1, the anteromedian fossettid is present (Figure 14-B2). Posteroflexid present in m3.

***Oecomys* species D**

Geographic distribution: Apparently restricted to the region between the rivers Tapajós and Xingu (Figure 8).

Morphological description: This species is genetically closely related to *Oecomys bicolor* and *Oecomys cleberi*; however, it is morphologically more similar to *Oecomys rutilus*. This is the smallest species we analyzed (Table 10). Head and dorsal fur is smooth orange-brownish colored, reaching about 6 mm in length. Flank is brighter than dorsum. Ventral surface is white to the roots. Females are smaller and darker than males, with dorsal fur reaching about 4 mm in length. The larger mystacial vibrissa is dark brown and reaches 34 mm in length, surpassing the ear. Ear is about 15 % of head and body length, dark brown with orange hairs on inner surface. Dark brown tail longer than head and body length, about 110 %, with squared to rounded scales arranged in circles. The central hair of each scale is longer and thicker than lateral ones, reaching more than three scales, while lateral hairs reach no more than two scales. Pencil is about 6.5 mm in length. Body pelage extends 8 – 10 mm over proximal portion of taxidermyzed tail. Feet are short, about 23 % of head and body length, with six plantar pads well developed, *squamae* on plantar surface and dermal folds on fingers. Claws are curved with densely pure white ungual tufts covering almost all claws in length. Fingers are covered mainly with pure whit hairs. Metatarsals are covered by mainly pure brown or brown-based hairs, which lead to a conspicuous spot on metatarsals.

Oecomys species D has a small, delicate and inflate skull (Figures 12K and 13K), with small nasal bones and the nasal-frontal suture V-shaped, continuous with the frontal-maxillary suture. Supraorbital ridge is very slightly developed, almost absent. Frontal-parietals and frontal-squamosal sutures are continuous. Parietals broadly extend upon squamosal bone. Interparietal bone is very large, wider than longer, occupying all the braincase breadth. There is no projection of the anterior edge of the zygomatic plate. The palatal bridge exhibits one large or two smaller posterolateral pits on each side. Incisive foramina are long and narrow. Mesopterygoid fossa is broad, its anterior edge is rounded and generally do not surpass the posterior border of the maxillary bone and its roof is totally ossified. Alisphenoid strut is always absent and the anterior opening of the alisphenoid canal is always present. The subsquamosal process is very thin and longer and the subsquamosal fenestra is always moderate in size. This species showed the pattern 1 of carotid and stapedial circulatory system described by Voss (1988). Generally the wall of the internal carotid canal composed only by the bullae and the basioccipital bone, however the periotic can compose this wall too. Mastoid bone has fenestra on top that varies from small to moderate in size. The mental foramen opens laterally. Both upper and lower masseteric ridges join only on anterior tip of each ridge and do

not surpass the m1 alveoli. The capsular process of the lower incisor alveoli present but slightly curved.

There is no accessory labial root on M1. On M1, the anteroflexus is always present (Figure 14-K1). On M2 the protoflexus and an accessory loph posterior to paracone are present. The mesoflexus on M2 is usually a single labial fossette. Hypoflexus in M3 is present. First and second lower molars (m1 and m2) usually do not show accessory roots or divisions of the anterior root, thus each molar presents only two roots, however one specimen (MG39770) showed an accessory labial root on m1. The anteromedian fossettid is present on m1 (Figure 14-K2). Posteroflexid is very deep in m3.

CONCLUSIONS

Since Hershkovitz's (1960) review of *Oecomys*, several studies based on morphological, molecular and karyotypical data showed that the species diversity inside the genus is larger than the currently recognized. Our study corroborates this fact, since we were able to recognize eleven species occurring in the eastern Brazilian Amazon forest, five of which are already expected to occur in this area (*Oecomys auyantepui*, *O. bicolor*, *O. paricola*, *O. rex*, and *O. rutilus*), two have never been recorded in the Amazonian region (*Oecomys catherinae*, from the Atlantic forest, and *O. cleberi*, known only from its type locality in the gallery forests of the savannas in Central Brazil), and four probably represent new species or species currently hidden in the taxonomy as synonyms, herein named *Oecomys* sp. A, *Oecomys* sp. B, *Oecomys* sp. C, and *Oecomys* sp. D. This work is also a starting point to solve problems faced by the specialist who needs to identify specimens of *Oecomys* at the species level based on morphological and morphometric characters. Despite of being able to provide diagnostic characters to most taxa herein recognized, examination of types are still necessary to name all of them appropriately. In addition, based on high nucleotide divergence (7.5 %) and the phylogenetic position of specimens identified as *O. bicolor* in our phylogenetic analysis, we agree with previous molecular studies that *Oecomys bicolor* represents a species complex, which awaits more refined and denser sampled analysis to be assessed.

Our study contributes significantly to the knowledge of relationships among the species of *Oecomys*, as it is the most comprehensive phylogenetic study on the genus to date,

including 11 of the 16 currently recognized species plus seven probably new species from a broad geographical area, with emphasis on the eastern Brazilian Amazon region.

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APPENDIX 1

GAZETTEER

Brazil

Acre

[1] Marechal Thaumaturgo, Seringal Oriente, Rio Juruá. 08º48’S 72º46’W (Paynter & Traylor 1991).

Amapá

[2]Amapá. 03º03'N 50º48'W (Gardner 2007).

[3] Ferreira Gomes, Caldeirão.

[4] Ferreira Gomes, Rio Araguari. 00º48'N 51º08'W (Gardner 2007).

[5] Itapoã, Fazenda Itapoã, AP-156, km 380. 02º05'N 50º55'W (Gardner 2007).

[6] Laranjal do Jari, Cachoeira Santo Antônio, TCD/AP. 00º35'S 52º14'W (Collector).

[7] Laranjal do Jari, Iratapuru.

[8] Laranjal do Jari, Resex Cajari, Marinho. 00º35'S 52º38'W (Collector).

[9] Mazagão, Igarapé Rio Branco, alto Rio Maracá. 00º32'N 52º12'W (Gardner 2007).

[10] Mazagão, margem esquerda do Rio Maracá. 00º32'S 51º26'W (Paynter & Traylor 1991).

[11] Oiapoque, Vila Velha do Cassiporé. 03º13'N 51º13'W (Gardner 2007).

[12] Porto Grande, Assentamento Nova Canaã.

[13] Porto Grande, Fazenda Matapi.

[14] Porto Grande, Floresta Nacional do Amapá, Igarapé Santo Antônio. 01º05'N 51º53'W (Collector).

[15] Serra do Navio, Parque Nacional Montanhas do Tumucumaque, Rio Anacui. 01º50'N 52º44'W (Collector).

[16] Serra do Navio, Parque Nacional Montanhas do Tumucumaque, Rio Mutum. 01º13'N 51º55'W (Collector).

[17] Serra do Navio, PCH Capivara, Rio Amapari. 00º59'N 52º06'W (Collector).

[18] Serra do Navio, Rio Amapari. 00º59'N 52º03'W (Gardner 2007).

[19] Tartarugalzinho, Fazenda Asa Branca.

[20] Tartarugalzinho, Fazenda São Bento, AMCEL III. 01º16'N 50º46'W (Collector).

Amazonas

[21] Barcelos, Estirão do Equador, Rio Javari. 04º27'S 71º30'W (Paynter & Traylor 1991).

[22] Humaitá, BR-230, Transamazônica, Km 986. 07º31'S 63º02'W (Gardner 2007).

[23] Itacoatiara, Cachoeira Lindóia. 02º58'S 58º57'W (Collector).

[24] Lago do Batista, Sul do Rio Amazonas. 03º18'S 58º15'W (Gardner 2007).

[25] Manaus. 03º08'S 60º01'W (Gardner 2007).

[26] Manaus, estrada Manaus-Itacoatiara, km 46.

[27] Maraã, Comunidade Boa Esperança, Igarapé Juá Grande, Reserva de Desenvolvimento Sustentável Amanã. 02º39'S 67º29'W (GeoNet 2009).
[28] Maraã, Setor Coraci, rio Coracizinho, Reserva de Desenvolvimento Sustentável Amanã. 01º50'S 55º11'W (GeoNet 2009).
[29] Rio Juruá. 06º45'S 68º00'W (Gardner 2007).
[30] Tefé, Estação Ecológica Mamirauá, Rio Japurá. 03º22'S 64º42'W (GeoNet 2009).
[31] Uarini, margem esquerda médio rio Solimões, Ilha do Ferro - Reserva de Desenvolvimento Sustentável Mamirauá. 02º55'S 65º08'W (GeoNet 2009).
[32] Urucará. 02º23'S 57º38'W (Collector).

Espírito Santo
[33] Águia Branca, Águas Claras, Fazenda do Zequinha Manduca. 18º52'S 40º48'W (Collector).
[34] Cariacica, Alto Alegre, Reserva Biológica de Duas Bocas. 20º16'S 40º31'W (Collector).

Goiás
[35] Barra do Rio São Domingos. 15º28’S 44º24’W (Paynter & Traylor 1991).

Mato Grosso
[36] Apiacás. 09º32'S 57º27'W (GeoNet 2009).
[37] Aripuanã, Cidade Laboratório de Humboldt. 09º10'S 60º38'W (Gardner 2007).
[38] Cláudia. 11º29'S 54º53'W (GeoNet 2009).
[39] Querência, Fazenda Tanguro. 12º49'S 52º21'W (Collector).
[40] Vila Rica. 10º00'S 51º06'W (GeoNet 2009).

Mato Grosso do Sul
[41] Brasilândia, Fazenda Barma.

Pará
[42] Alenquer, Estação Ecológica Grão-Pará Sul. 00º09'S 55º11'W (Collector).
[43] Almeirim, Cachoeira Santo Antônio, TCD/PA. 00º35'S 52º31'W (Collector).
[44] Almeirim, Floresta Estadual Paru, margem direita do rio Paru de Leste. 00º56'S 53º14'W (Collector).
[45] Almeirim, Itapeuara. 00º27'S 52º40'W (Collector).
[46] Almeirim, Reserva Biológica Maicuru. 00º49'N 53º55'W (Collector).
[47] Altamira, 19 Km S e 18 Km O de Altamira, Agrovila União. 03º22'S 52º23'W (Specimen label).
[48] Altamira, 54 km S e 150 km O de Altamira, gleba 61, lote 02. 03º41'S 53º45'W (Specimen label).
[49] Anapu, Caracol, margem direita do Rio Xingú. 03º17'S 51º40'W (Specimen label).
[50] Barcarena. 01º30'S 48º40'W (Gardner 2007).
[51] Belém, Parque Ambiental de Belém, Utinga. 01º27'S 48º29'W (Gardner 2007).

[52] Belterra, 26 Km S e 25 Km O de Santarém. 02º38'S 54º57'W (Gardner 2007).

[53] BR-010, km 87-97. 01º40'S 47º47'W (Gardner 2007).

[54] Cachoeira do Espelho, margem direita do Rio Xingú. 03º39'S 52º22'W (Collector).

[55] Chaves, Fazenda Tauarí, margem direita do baixo rio Cururu. 00º39'S 50º11'W (GeoNet 2009).

[56] Faro, Floresta Estadual de Faro, margem esquerda do rio Nhamundá, ca 70 km NW de Faro. 01º42'S 57º12'W (Collector).

[57] Igarapé Jaramacaru.

[58] Ilha de Marajó. 01º00'S 49º30'W (Gardner 2007).

[59] Itaituba, km 446, BR165, Santarém-Cuiabá. 05º10'S 56º00'W (Gardner 2007).

[60] Itaituba, Parque Nacional da Amazônia, 56 km. 03º50'S 56º15'W (Gardner 2007).

[61] Itaituba, Transamazônica. 04º17'S 55º59'W (Paynter & Traylor 1991).

[62] Itaituba. 04º17'S 55º59'W (Paynter & Traylor 1991).

[63] Itupiranga, 26 Km N e 30 Km W de Marabá, gleba 05, lote 05. 05º06'S 49º24'W (Specimen label).

[64] Itupiranga, Fazenda Mineira, km 42. 05º06'S 49º20'W (Paynter & Traylor 1991).

[65] Jacareacanga, Flexal, Km 212. 05º34'S 57º13'W (Gardner 2007).

[66] Juruti, Adutora Capiranga.

[67] Juruti, Área de influência do Projeto Juruti ALCOA.

[68] Juruti, Comunidade Barroso. 02º27'S 56º00'W (Specimen label).

[69] Juruti, Mutum (antigo acampamento da ALCOA). 02º36'S 56º11'W (Specimen label).

[70] Juruti, Platô Capiranga. 02º30'S 56º11'W (Specimen label).

[71] Juruti, Ramal Galiléia.

[72] Juruti, Ramal Pacoval.

[73] Mamiá, LT-Oriximiná-Macapá. 04º01'S 62º52'W (Collector).

[74] Marabá, 73 Km N e 45 Km W de Marabá, perto de Jatobal, gleba 29, lote 03. 04º01'S 49º32'W (Specimen label).

[75] Marabá, Floresta Nacional Tapirapé-Aquiri, Projeto Salobo CVRD, Área Controle. 05º50'S 50º32'W (Collector).

[76] Marabá, Floresta Nacional Tapirapé-Aquiri, Projeto Salobo CVRD, Barragem de Finos. 05º49'S 50º29'W (Collector).

[77] Marabá, Floresta Nacional Tapirapé-Aquiri, Projeto Salobo CVRD, Barragem de Rejeitos. 05º46'S 50º30'W (Collector).

[78] Marabá, Floresta Nacional Tapirapé-Aquiri, Projeto Salobo CVRD, Cava da Mina. 05º47'S 50º32'W (Collector).

[79] Marabá, Floresta Nacional Tapirapé-Aquiri, Projeto Salobo CVRD, Igarapé Mano. 05º46'S 50º33'W (Collector).

[80] Marabá, Serra dos Carajás. 06º00'S 51º20'W (GeoNet 2009).

[81] Melgaço, Estação Científica Ferreira Penna, Caiçara. 01º44'S 51º27'W (Abrahim & Bonaldo 2008).

[82] Monte Alegre. 02º01'S 54º04'W (Paynter & Traylor 1991).

[83] Novo Progresso, W de Castelo dos Sonhos, BR-163, 940km N de Cuiabá. 08º20'S 55º12'W (Specimen label).

[84] Óbidos, Estação Ecológica Grão-Pará Centro. 00º37'N 55º43'W (Collector).

[85] Óbidos, Floresta Estadual do Trombetas. 00º57'S 55º31'W (Collector).

[86] Oriximiná, Estação Ecológica Grão-Pará Norte. 01º17'N 58º41'W (Collector).

[87] Oriximiná, Porto Trombetas, Igarapé Teófilo. 01º46'S 56º33'W (Specimen label).

[88] Oriximiná, Porto Trombetas, mineração bauxita, Rio Saracuzinho, km 7, afluente do Rio Trombetas.

[89] Oriximiná, Porto Trombetas, Platô Aviso. 01º44'S 50º30'W (Specimen label).

[90] Oriximiná, Porto Trombetas, Platô Bela Cruz. 01º44'S 56º30'W (Specimen label).

[91] Oriximiná, Porto Trombetas, Platô Cipó. 01º44'S 56º36'W (Specimen label).

[92] Oriximiná, Porto Trombetas, Platô Greig. 01º50'S 56º31'W (Specimen label).

[93] Oriximiná, Porto Trombetas, Platô Saracá. 01º41'S 54º59'W (Specimen label).

[94] Oriximiná, Porto Trombetas, Platô Teófilo. 01º45'S 56º31'W (Specimen label).

[95] Paragominas, Fazenda Rio Capim.

[96] Paragominas. 03º00'S 47º18'W (Paynter & Traylor 1991).

[97] Parauapebas, Serra Norte, 145 km SW of Marabá. 06º00'S 50º18'W (Gardner 2007).

[98] Portel, Floresta Nacional de Caxiuanã, Plot do PPBio. 01º57'S 51º36'W (Abrahim & Bonaldo 2008).

[99] Santarém, Curuá-Una. 44 Km S e 40 Km E de Santarém. 02º50'S 54º22'W (Specimen label).

[100] Santarém, estrada Santarém-Cuiabá, BR-163, km 84-217.

[101] São Félix do Xingú, Reserva Indígena Gorotire, próximo a Gradaús, Rio Fresco, afluente do Rio Xingú. 07º43'S 51º11'W (Gardner 2007).

[102] Terra Santa, Comunidade Maracana, Igarapé Xingú. 02º06'S 56º36'W (Collector).

[103] Tucuruí, Igarapé Canoal, 30 Km S de Tucuruí, margem direita do Rio Tocantins (inundado). 04º06'S 49º38'W (GeoNet 2009).

[104] Villa Braga, Rio Tapajós. 04º25'S 56º17'W (Gardner 2007).

[105] Vitória do Xingú, Bom Jardim, margem esquerda do Rio Xingú. 03º24'S 51º40'W (Specimen label).

Rondônia

[106] Foz do Rio Jamari. 08º27'S 63º30'W (Paynter & Traylor 1991).

[107] Parque (Serra) dos Pacaás Novos. 10º45'S 64º15'W (GeoNet 2009).

[108] Santa Barbara.

[109] UHE Samuel. 08º45'S 63º28'W (Paynter & Traylor 1991).

[110] Vilhena, Fazenda Planalto, km 53, BR 364. 12º43'S 60º07'W (Paynter & Traylor 1991).

Roraima

[111] UHE Alto Jatapu, São João da Baliza, 30 km do Entre Rios. 00º31'N 59º20'W (GeoNet 2009).

Sergipe

[112] Areia Branca, Estação Ecológica Serra de Itabaiana. 10º40'S 37º25'W (Gardner 2007).

Tocantins

[113] Aliança do Tocantins, Fazenda Boa Esperança. 11º08'S 48º48'W (Gardner 2007).

APPENDIX 2

Nominal taxa associated to *Oecomys* according to Musser & Carleton 2005 and Carleton *et al.* 2009, and its type-localities. Taxa currently recognized as species are marked with an asterisk (*).

Nominal Taxa	Type Locality
*auyantepui** Tate, 1939	Venezuela, Bolívar, eastern Caroni river, Mt. Auyán-Tepuí, 1100 m.
*bicolor** Tomes, 1860	Ecuador, Morona-Santiago, Gualaquiza, Gualaquiza river, 885 m.
benevolens Thomas, 1901	Bolivia, La Paz, Chimate, upper Beni river, 700 m.
dryas Thomas, 1900	Ecuador (norwestern), Imbabura, Paramba, Mira river, 1100 m.
endersi Goldman, 1933	Panama, Barro Colorado Island, Canal zone.
florenciae J.A. Allen, 1916	Colombia, Caquetá, upper Caquetá river, Orteguaza river, Florencia.
milleri J.A. Allen, 1916	Brazil, Mato Grosso, Barão de Melgaço, Madeira, upper Jy-Paraná, Rio Conguiaru.
nitedulus Thomas, 1910	Guyana, Demerara, lower Essequibo River, 13 milhas from mouth.
occidentalis Hershkovitz, 1960	Ecuador (norwestern), Imbabura, Mira River, Paramba, 1100 m.
phelpsi Tate, 1939	Venezuela, Bolívar, eastern Caroni river, Mt. Auyán-Tepuí, 1100 m.
rosilla Thomas, 1904	Venezuela, Bolívar, Orinoco River, lower Caura River, La Unión.
trabeatus G.M. Allen & Barbour, 1923	Panama (eastern), Darién, Jesuíto (ou Jesusito) River.
*catherinae** Thomas, 1909	Brazil, Santa Catarina, Joinville.
bahiensis Hershkovitz, 1960	Brazil, Bahía, lhéus.
cinnamomeus Pictet & Pictet, 1844	Brazil, Bahía, lhéus.
*cleberi** Locks, 1981	Brazil, Distrito Federal, Universidade de Brasília, Fazenda Água Limpa.
*concolor** Wagner, 1845	Brazil, Amazonas, Curicuriari River, upper Negro River, near São Gabriel.
marmorsurus Thomas, 1899	Colombia (eastern), Vichada, Orinoco River, Maipures.
*flavicans** Thomas, 1894	Venezuela, Mérida, 1600 m.
illectus Bangs, 1896 ou 1898	Colombia, Magdalena, Sierra Nevada de Santa Marta, Pueblo Viejo, 853 m.
mincae J.A. Allen, 1913	Colombia, Magdalena, Sierra Nevada de Santa Marta, Minca.
*mamorae** Thomas, 1906	Bolivia, Cochabamba, alto Río Mamoré, Mosetenes.
*paricola** Thomas, 1904	Brazil, Pará, Igarapé Assú, 50 m.
*phaeotis** Thomas, 1901	Peru, Puno, upper Inambari River, Sagrario, 1000 m.

Continuity of appendix 2

Nominal taxa	Type-locality
*rex** Thomas, 1910	Guyana, Demerara, Supenaam River.
regalis Hershkovitz, 1960	Guyana, Demerara, Supenaam River.
*roberti** Thomas, 1904	Brazil, Mato Grosso, Santa Anna da Chapada (=Chapada dos Guimarães), 800 m.
guianae Thomas, 1910	Guyana, Demerara, Supenaam River.
tapajinus Thomas, 1909	Brazil, Pará, Tapajós River, Jamanchin River, Santa Rosa.
*rutilus** Anthony, 1921	Guyana, Mazaruni-Potaro, Kartabo.
*speciosus** J.A. Allen & Chapman, 1893	Trinidad, Princes Town.
caicarae J.A. Allen, 1913	Venezuela, Bolívar, Orinoco River, Caicara.
trichurus J.A. Allen, 1899	Colombia, Magdalena, Sierra Nevada de Santa Marta, El Líbano, near Bonda.
*superans** Thomas, 1911	Ecuador, Pastaza, Bobonaza River, Canelos, 640 m.
melleus Anthony, 1924	Ecuador (eastern), Santiago-Zamora, Zamora, 1000 m.
palmeri Thomas, 1911	Ecuador, Pastaza, Bobonaza River, Canelos, 640 m.
*trinitatis** J.A. Allen & Chapman, 1893	Trinidad, Princes Town.
frontalis Goldman, 1912	Panama, Corozal, Canal Zone.
fulviventer J.A. Allen, 1899	Venezuela, Sucre, Cumanacoa, Manzanares River, Quebrada Seca.
helvolus J.A. Allen, 1913	Colombia, Meta, Meta River, Villavivencio.
klagesi J.A. Allen, 1904	Venezuela, Bolívar, lower Caura River, El Llagual (Yagual), near Maripa.
osgoodi Thomas, 1924	Peru, Amazonas, Moyobamba, 820 m.
palmarius J.A. Allen, 1899	Venezuela, Sucre, Cumanacoa, Manzanares River, Quebrada Seca.
splendens Hayman, 1938	Trinidad (southeastern), Mayaro.
subluteus Thomas, 1898	Colombia, Cundinamarca, western of Cordilheira Oriental.
tectus Thomas, 1901	Panama, Chiriquí, Bugaba (Bugava), 250 m.
vivencianus J.A. Allen, 1913	Colombia, Meta, Meta River, Villavivencio.
*sydandersoni** Carleton, Emmons & Musser, 2009	Bolivia, Santa Cruz, Velasco, El Refugio Huanchaca, 210 m.

APPENDIX 3

Specimens analyzed for each species, with localities, specimen preparationtype, collection number. Specimens tagged with an asterisk (*) have cytochrome-b sequences. Locality numbers correspond to the Gazeetter. **Legend**: **1** – Number of dry skins; **2** – Number of skulls; **3** – Number of fluid preserved material; **4** – Number of cytochrome-b sequences; **X** – No GenBank accession number; **IEPA** – Instituto de Pesquisas Científicas e Tecnológicas do Amapá; **MG** – Museu Paraense Emilio Goeldi; **MN** – Museu Nacional do Rio de Janeiro; **MZ** – Museu de Zoologia da Universidade de São Paulo; **BAR** – Specimens from Universidade Federal do Pará; **UFES** – Universidade Federal do Espírito Santo, Coleção de Tecidos Animais.

Species	Locality	Material				Specimens
		1	2	3	4	
auyantepui	[7]	-	1	-	-	IEPA2449.
	[8]	2	3	1	1	IEPA1134; IEPA2438; IEPA2439*.
	[10]	1	1	-	-	MG2529
	[11]	4	-	-	-	MN20661; MN20671; MN20672; MN20686.
	[17]	-	2	1	-	IEPA1623; IEPA2452.
	[18]	-	1	-	-	MG13132
	[21]	1	1	-	-	MN20693.
	[23]	1	1	-	1	MG40055*.
	[25]	2	2	-	-	MN19617; MN19618.
	[26]	1	1	-	-	MG7169.
	[42]	3	3	-	3	MG39930*; MG39931*; MG39932*.
	[44]	2	2	-	2	MG40455*; MG40456*.
	[45]	2	2	-	2	IEPA2412*; IEPA2413*.
	[56]	3	-	-	2	MG39910; MG39911*; MG39968*.
	[73]	2	2	-	2	IEPA2444*; IEPA2446*.
	[82]	1	-	-	-	MZ20580.
	[84]	5	6	1	5	MG40457*; MG40458*; MG40459*; MG40460; MG40461*; MG40649*.
	[85]	10	8	-	8	MG39914*; MG39917*; MG39921*; MG39924*; MG39925*; MG39926*; MG39927*; MG39938*; MG40003; MG40010.
	[86]	6	6	-	6	MG40447*; MG40448*; MG40449*; MG40450*; MG40452*; MG40453*.
	[87]	1	1	-	1	MG39798*.
	[88]	1	1	-	-	MG10112.
	[89]	2	3	1	-	MG39816; MG39817; MG39827.
	[90]	2	3	1	3	MG39793*; MG39794*; MG39836*.
	[91]	1	1	-	1	MG39804*.
	[92]	1	1	-	-	MG39799; MG39801.
	[93]	1	2	1	2	MG39795*; MG39831*.
	[102]	4	4	-	4	MG40076*; MG40078*; MG40084*; MG40085*.
bicolor	[1]	1	1	-	-	MZ20502.
	[3]	1	1	-	-	IEPA2451.
	[4]	6	6	-	5	IEPA2340*; IEPA2358; IEPA2383*; IEPA2387*; IEPA2389*; IEPA2393; IEPA2395*.
	[5]	7	4	-	-	MG34312; MG34315; MG34325; MG34326; MG34338; MG34353; MG34564.
	[6]	1	1	-	-	IEPA2431.
	[7]	1	1	-	-	IEPA2411.
	[9]	5	3	-	-	MN20660; MN20663; MN20665; MN20666; MG2499.
	[10]	1	-	-	-	MN20672.
	[13]	-	2	2	1	IEPA1637; IEPA2031*.
	[14]	-	1	1	-	IEPA622.
	[17]	-	1	1	-	IEPA1622.
	[18]	5	2	-	-	MG6690; MG6791; MG15136; MZ20498; MZ20499.
	[19]	1	1	-	-	MG34081.

Continuity of Appendix 3

Species	Locality	Material				Specimens
		1	2	3	4	
bicolor	[20]	3	3	-	1	IEPA1612; IEPA2453; IEPA2436*.
	[21]	1	1	-	-	MN20696.
	[23]	1	1	-	1	MG40061*.
	[29]	2	1	-	-	MZ888; MZ889.
	[36]	1	-	-	1	MZ29523*.
	[42]	1	1	-	1	MG39933*.
	[66]	1	1	-	-	MG40673.
	[67]	11	10	-	-	MG38393; MG38397; MG38399; MG38405; MG38412; MG38413; MG38414; MG38416; MG38417; MG38420; MG38422.
	[68]	4	4	-	-	MG38369; MG38371; MG38390; MG38392.
	[69]	2	2	-	-	MG38530; MG38531.
	[70]	5	5	-	1	MG38520; MG38524; MG38532; MG38682*; MG40672; MG38678.
	[71]	1	1	-	1	MG40667*.
	[86]	1	1	-	1	MG40451*.
	[106]	2	2	-	-	MZ20587; MZ20588.
	[108]	1	-	-	-	MZ20087.
	[111]	1	1	-	-	MN51655.
catherinae	[33]	-	-	-	1	UFES245*.
	[34]	-	-	-	1	UFES519*.
	[35]	-	1	-	-	MG10901.
	[37]	4	6	-	1	MG12652; MG12690; MG12691; MG13172; MG13173; MZ29532*.
	[40]	1	-	-	1	MZ29533*.
	[47]	-	1	-	-	MG10913.
	[48]	-	1	-	-	MG10911.
	[65]	-	1	-	-	MG13169.
	[76]	3	-	-	3	MG39897*; MG39899*; MG39900*.
	[78]	3	3	-	3	MG39901*; MG39903*; MG39909*.
	[80]	2	2	-	1	MG38898*; MG38976.
	[100]	-	1	-	-	MG8229.
	[110]	1	1	-	-	MG34224.
	[112]	5	1	-	-	MG24553; MG24554; MG24561; MG24562; MG24563.
cleberi	[39]	4	4	-	4	MG39934*; MG39935*; MG39936*; MG39937*.
	[49]	1	1	-	-	MG39785.
	[54]	1	1	-	-	MZ27130.
	[77]	1	1	-	1	MG39891*.
	[80]	1	1	-	1	MG39040*.
	[98]	1	1	-	1	MG40861*.
	[101]	4	4	-	-	MG1295; MG1302; MZ20500; MZ20501.
paricola	[49]	3	6	3	4	MG39773*; MG39775; MG40736*; MG40737*; MG40738*; MG40739.
	[50]	5	5	-	5	BAR006*; BAR013*; BAR017*; BAR023*; BAR029*.
	[51]	18	17	-	6	MG2477; MG2584; MG2593; MG2605; MG2610; MG2614; MG2615; MG2632; MG2635; MG2647; MG38659*; MG38664*; MG39699*; MG39701*; MG39703; MG39705*; MG39708*; MG39709; MG40732; MZ23179.
	[53]	15	45	-	-	MG8382; MG8438; MZ10399; MZ20503; MZ20504; MZ20505; MZ20506; MZ20507; MZ20508; MZ20509; MZ20511; MZ20512; MZ20513; MZ20516; MZ21986; MZ21987; MZ22516; MZ22517; MZ23145; MZ23146; MZ23147; MZ23150; MZ23151; MZ23152; MZ23153; MZ23154; MZ23155; MZ23156; MZ23839; MZ24121; MZ24122; MZ24123; MZ24124; MZ24125; MZ24126; MZ24127; MZ24128; MZ24129; MZ24130; MZ24131; MZ24132; MZ24133; MZ24134; MZ24135; MZ24136.
	[54]	2	2	-	-	MZ27128; MZ27129.

Continuity of Appendix 3

Species	Locality	Material				Specimens
		1	2	3	4	
paricola	[55]	8	9	1	7	MG40842*; MG40843*; MG40844*; MG40845*; MG40846; MG40848*; MG40849*; MG40850; MG40851*.
	[58]	1	1	-	-	MN2000.
	[75]	3	3	-	3	MG39893*; MG39894*; MG39895*.
	[76]	2	1	-	2	MG39896*; MG39898*.
	[77]	3	3	-	3	MG39892*; MG39907*; MG39908*.
	[79]	2	2	-	2	MG39905*; MG39906*.
	[95]	1	-	-	-	MG38363.
	[97]	-	2	-	-	MG8741; MG8742.
	[98]	14	50	32	37	MG39939; MG39940; MG39941; MG39942; MG39943; MG39944*; MG39945*; MG39946; MG40740; MG40741; MG40742; MG40743; MG40744; MG40814; MG40815; MG40852*; MG40853*; MG40854*; MG40855*; MG40856*; MG40857*; MG40858*; MG40859*; MG40860*; MG40861*; MG40862*; MG40863*; MG40864*; MG40865*; MG40866*; MG40867*; MG40868*; MG40869*; MG40870; MG40871*; MG40872*; MG40873*; MG40874*; MG40875*; MG40876*; MG40877*; MG40878*; MG40879*; MG40880*; MG40881*; MG40882*; MG40883*; MG40884; MG40885*; MG40886*; MG40887*; MG40888*.
	[101]	1	1	-	-	MG1308.
rex	[6]	1	1	-	-	IEPA1539.
	[7]	1	1	1	2	IEPA2410*; IEPA2448*.
	[8]	-	1	1	1	IEPA2038*.
	[11]	-	2	-	-	MG8044; MG8047.
	[18]	2	1	-	-	MZ20517; MZ20518.
rutilus	[2]	2	2	-	-	MG1543; MG1545.
	[5]	2	2	-	-	MG34248; MG34259.
	[6]	1	1	-	-	IEPA1532.
	[8]	1	2	1	1	IEPA1620; IEPA2407*.
	[15]	2	2	-	1	IEPA2776; IEPA569*.
	[23]	1	1	-	1	MG40059*.
	[27]	1	-	-	-	MG36614.
	[32]	3	2	-	2	MG40062; MG40063*; MG40067*.
	[46]	1	-	-	1	MG40454*.
	[56]	1	-	-	1	MG39962*.
	[84]	2	1	-	2	MG40462*; MG40841*.
	[85]	12	11	1	11	MG39912*; MG39913*; MG39915*; MG39916*; MG39918*; MG39919*; MG39920; MG39922*; MG39923*; MG39928*; MG39929*; MG40004; MG40819*.
	[102]	1	1	-	1	MG40077*.
species A	[37]	-	1	-	-	MG13170.
	[65]	-	1	-	-	MG13167.
	[72]	2	2	-	1	MG40657*; MG40668.
species B	[5]	-	1	-	-	MG34506.
	[6]	1	2	1	1	IEPA1535*; IEPA1631.
	[7]	1	1	-	1	IEPA2409*.
	[9]	5	5	-	-	MG2505; MG2506; MG2507; MG2509; MN20649; MN20679.
	[20]	2	3	-	1	IEPA1611*; IEPA1613; IEPA1614.
	[27]	1	-	-	-	MG36866.
	[39]	1	1	-	-	MG40889.
	[45]	1	1	-	1	IEPA2414*.
	[48]	-	1	-	-	MG10912.
	[50]	1	-	-	1	BAR024*.
	[51]	5	3	-	2	MG12655; MG15261; MG15262; MG38668*; MG38675*.

Continuity of Appendix 3

Species	Locality	Material				Specimens
		1	2	3	4	
species B	[53]	6	5	-	-	MG15263; MZ20586; MZ23374; MG15264; MG8387; MZ20584; MZ20585.
	[54]	7	9	-	-	MZ27131; MZ27132; MZ27133; MZ27134; MZ27135; MZ27136; MZ27137; MZ27138; MZ27139; MZ27140.
	[55]	1	1	-	1	MG40847*.
	[64]	2	2	-	-	MG10145; MG10146.
	[74]	-	1	-	-	MG10924.
	[79]	2	2	-	2	MG39902*; MG39904*.
	[80]	1	1	-	1	MG38996*.
	[96]	1	1	-	-	MG12656.
	[99]	1	1	-	-	MG9081.
	[100]	-	2	-	-	MG15120; MG15121.
	[103]	1	1	-	-	MG11861.
	[113]	3	3	-	-	MG35228; MG35236; MG35241.
species C	[30]	1	1	-	-	MG24580.
	[31]	1	-	-	-	MG37157.
	[37]	1	1	-	-	MG12654.
	[38]	1	1	-	1	MZ29526*.
	[73]	1	1	-	1	IEPA2445*.
	[80]	1	1	-	-	MG39956.
species D	[38]	1	1	-	1	MZ29529*.
	[83]	1	1	-	-	MG39715.
	[105]	2	4	-	3	MG39770; MG40733*; MG40734*; MG40735*.

FIGURES

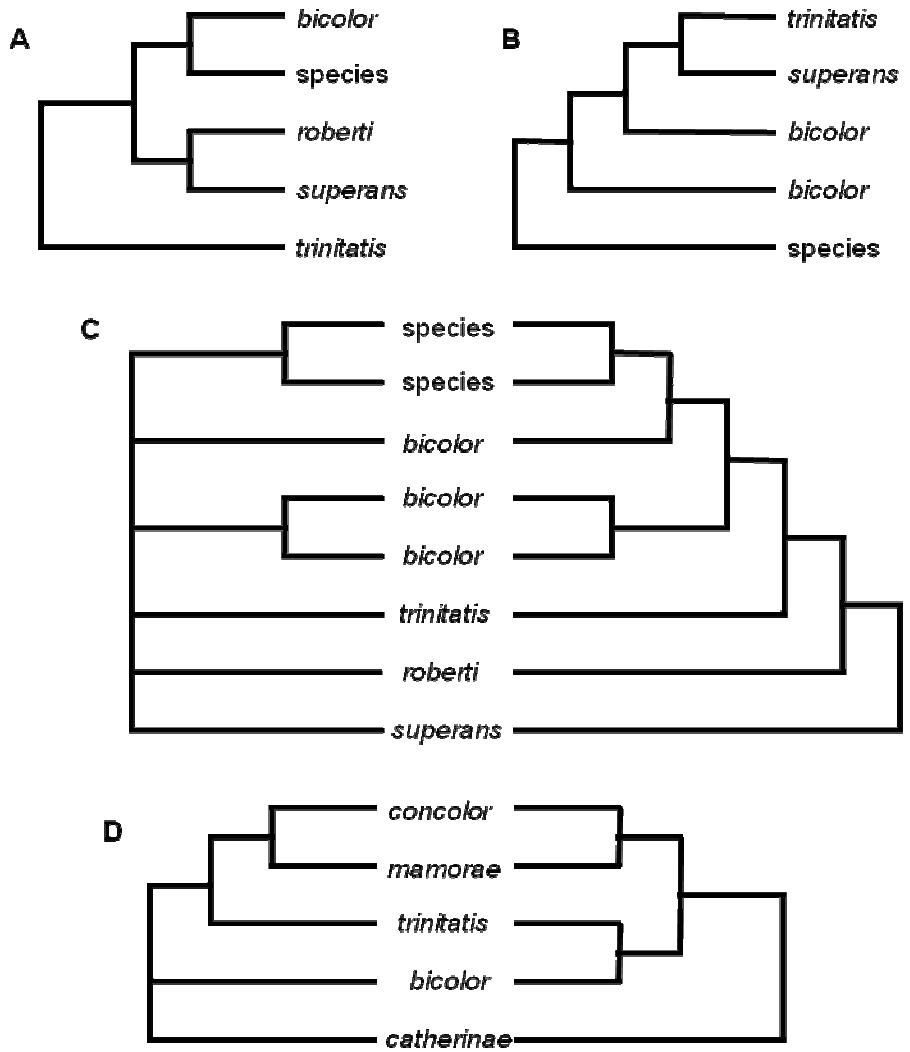

Figure 1 - Hypothesis of relationships among *Oecomys* species of relevant phylogenetic studies based on molecular e morphological data. **(A)** Maximum parsimony based on 801 bp of citochrome-b about the phylogenetic relationship among some Oryzomyini species (Patton & Da Silva, 1995; redrawn after their figure 9). **(B)** Analysis based on 801 bp of Cytocrome *b* of phylogenetic relationships among South American Sigmodontinae (Smith & Patton, 1999; redrawn after their figure 2). Consensus of two trees of a maximum parsimony analysis with all sites weighted equally and 556 parsimony informative sites; tree was rooted with seven species of North American Neotomyinae as outgroup. **(C)** Analysis based on 801 bp of Cytocrome *b* of phylogenetic relationship among Oryzomyinae (Andrade & Bonvincino, 2003; redrawn after their figure 4). The cladogram at the left show a strict consensus of three most-parsimonious trees with transversions weighted 5x higher than transitions. The cladogram at the right show a maximum likelihood tree with transversions weighted 5x higher than transitions. Trees were rooted with *Neotoma albigula* and *Scotinomys teguina* as outgroups. **(D)** Maximum parsimony of phylogenetic relationships among Oryzomyini based on 99 morphological characters and 1266 bp of IRBP partial gene (Weksler, 2006; redrawn after figures 34-39). Cladogram at the left shows the strict consensus of four minimum-length trees of only IRBP sequences with 204 parsimony informative characters. Cladogram at the right show the topology obtained from only morphological characters with polymorphic characters as composite or ordered; this is also the topology obtained from combined analysis.

Figure 2 - Bootstrap consensus tree (1000 replicates) of Neighbor Joining analysis from 104 sequences and 653 base pairs of cytochrome-*b*. Branches corresponding to partitions reproduced in less than 50% bootstrap replicates are collapsed. Bootstrap test > 50 % is shown above the branches and branch lengths > 0.005 is shown below. Branch lengths are the same as evolutionary distances computed using Kimura 2-parameter and are in the units of the number of base substitutions per site. The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.9321).

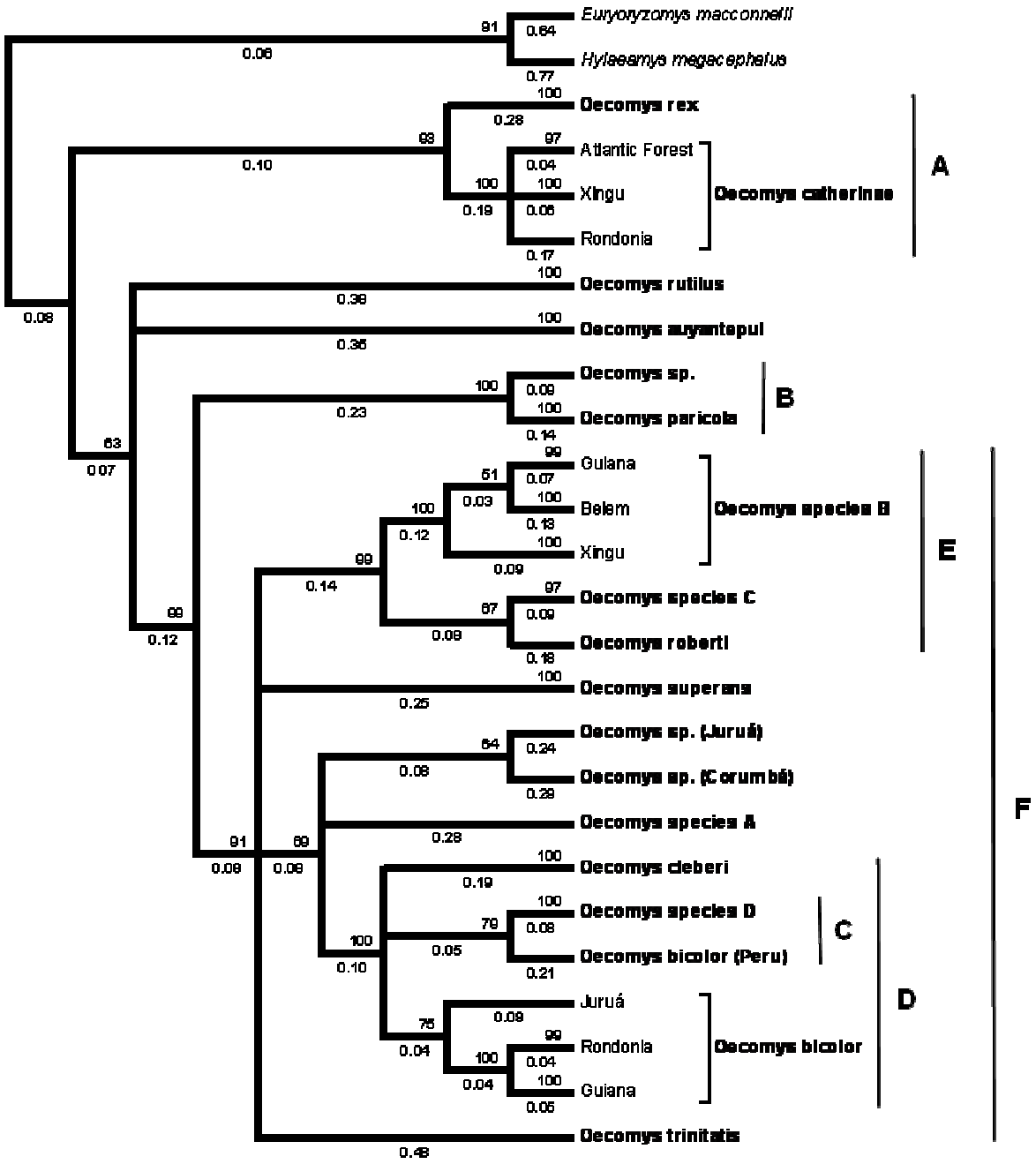

Figure 3 – Bayesian analysis consensus tree from 104 sequences and 653 base pairs of cytochrome-b. Statistical node support of Bayesian index > 50 % is shown above branch and branch length > 0.005 is shown below. Effective sample size (ESS) was 358,089 for combined runs. The rate variation among sites was modeled with a gamma distribution.

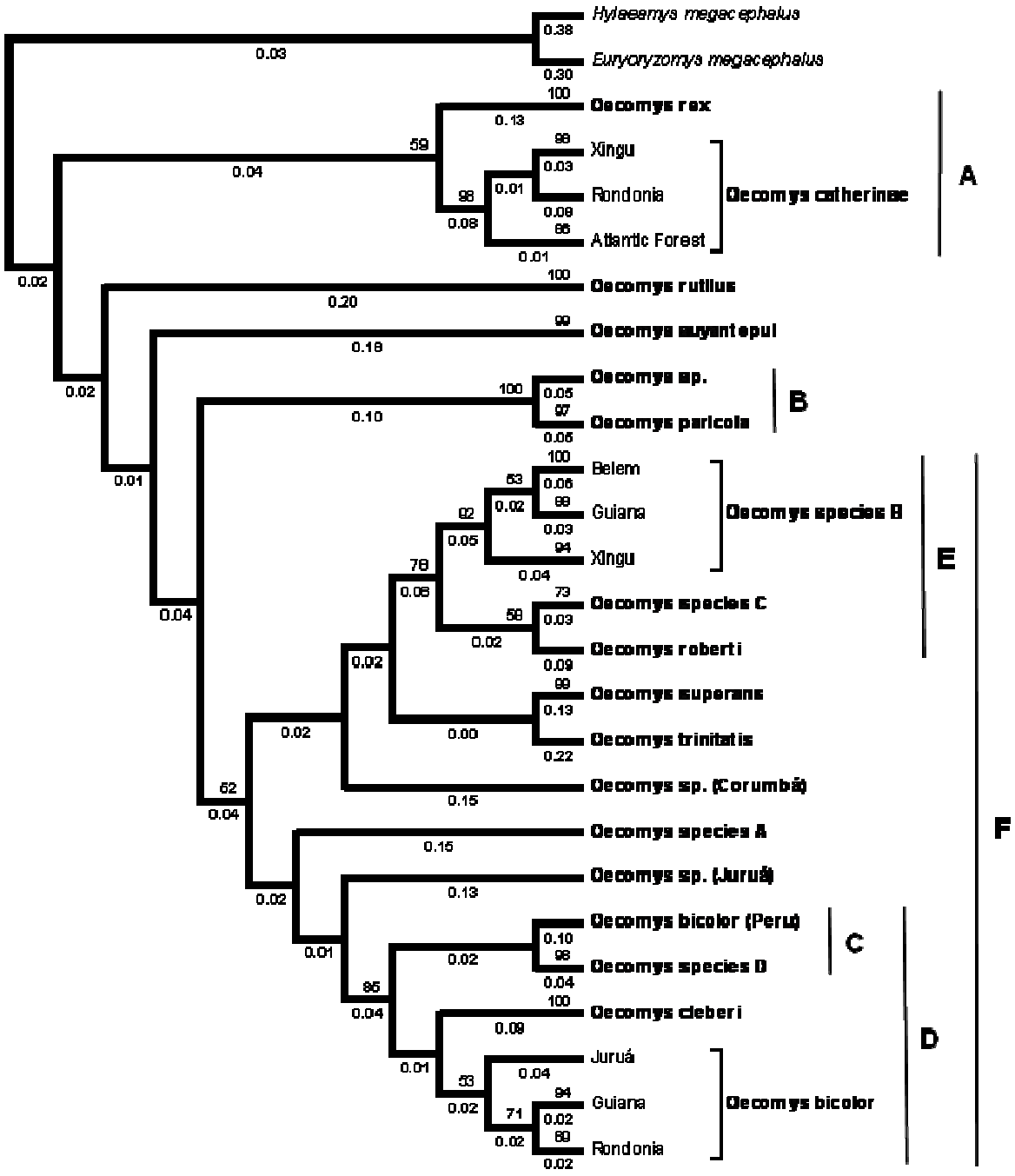

Figure 4 – Maximum likelihood analysis tree from 104 sequences and 653 base pairs of cytochrome-*b*. Bootstrap support > 50 % is shown above branch and branch length > 0.005 is shown below. GTR model of nucleotide substitution with gamma shape parameter = 0.9321 was used. Log-*L* = -5914.59594; Unconstrained-*L* = -2598.41172; tree size = 2.21315; GTR relative rate parameters: A – C 5.80913, A – G 22.91122, A – T 4.69410, C – G 0.00018, C – T 42.54165, G – T 1.00000.

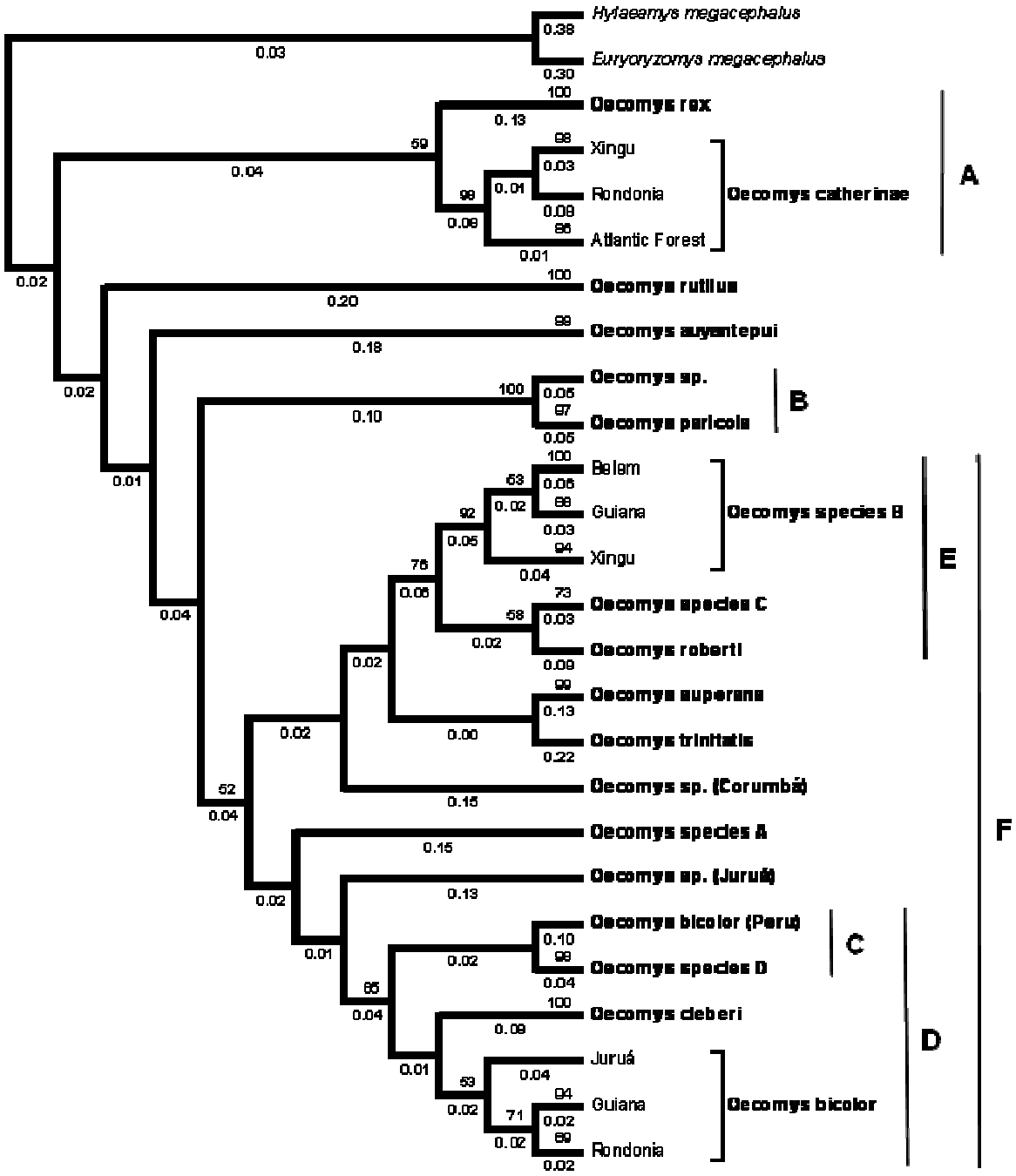

Figure 5 – Consensus of 50% major-rule tree of maximum parsimony analysis from 2,140,100 shorted trees, each 1059 steps long. The data set of 653 bp of cytochrome-b contained 258 variable sites and 207 of which were parsimony-informative. Each tree had an ensemble consistency index (CI) of 0.330, homoplasy index (HI) of 0.670, retention index (RI) of 0.833, rescaled consistency index (RC) of 0.275. Populations are also shown.

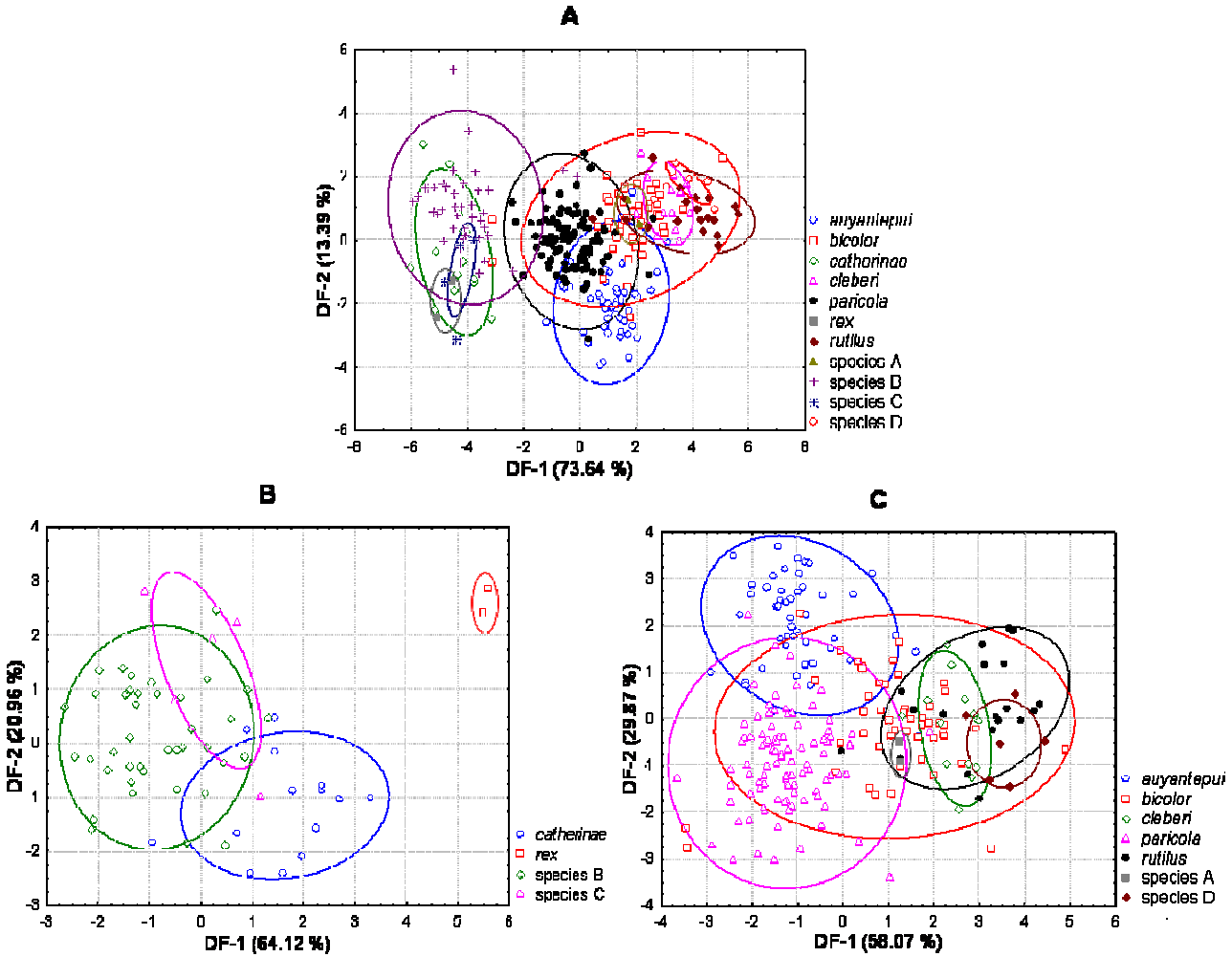

Figure 6 - Bivariate plots of canonical scores for the first two axes in comparisons among (**A**) all species from eastern Brazilian Amazon (Wilks' Lambda = 0.0238148; F (160, 2350) = 8.066392; p < 0.0000), (**B**) the four larger species (*Oecomys catherinae*, *O. rex*, *O.* species B and *O.* species C; Wilks' Lambda = 0.1163095; F (48, 125) = 2.779767; p < 0.0000), and (**C**) the remaining smaller species (*Oecomys auyantepui*, *O. bicolor*, *O. cleberi*, *O. paricola*; *O. rutilus*, *O.* species A and *O.* species D; Wilks' Lambda = 0.783764; F (96, 1230) = 7.273378; p < 0.0000), based on 16 log10 cranial variables. The percent of the total variation explained by each axis is indicated in each plot.

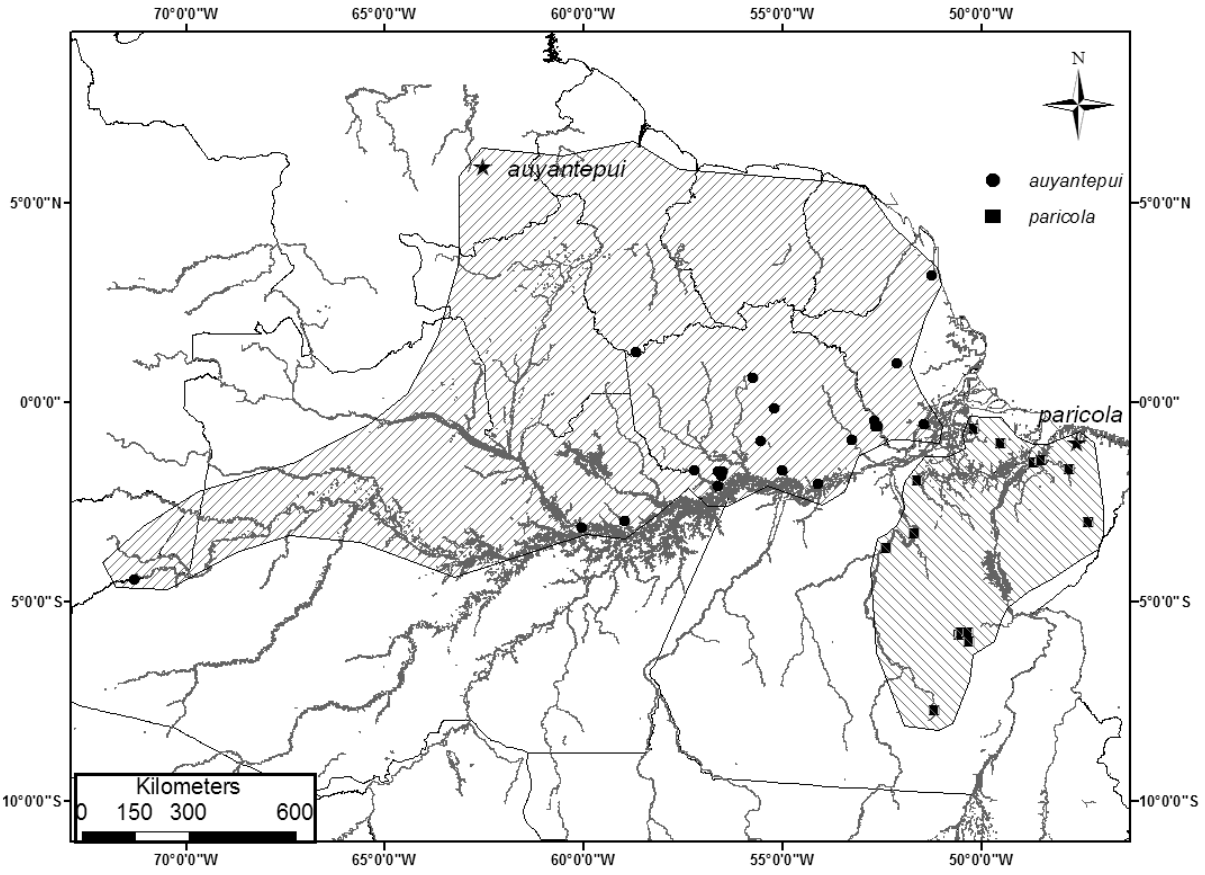

Figure 7 – Map of approximate distribution of *Oecomys auyantepui* (solid circles) and *Oecomys paricola* (solid squares); localities of analyzed specimens are plotted for each species, as well as the type locality from both (solid stars).

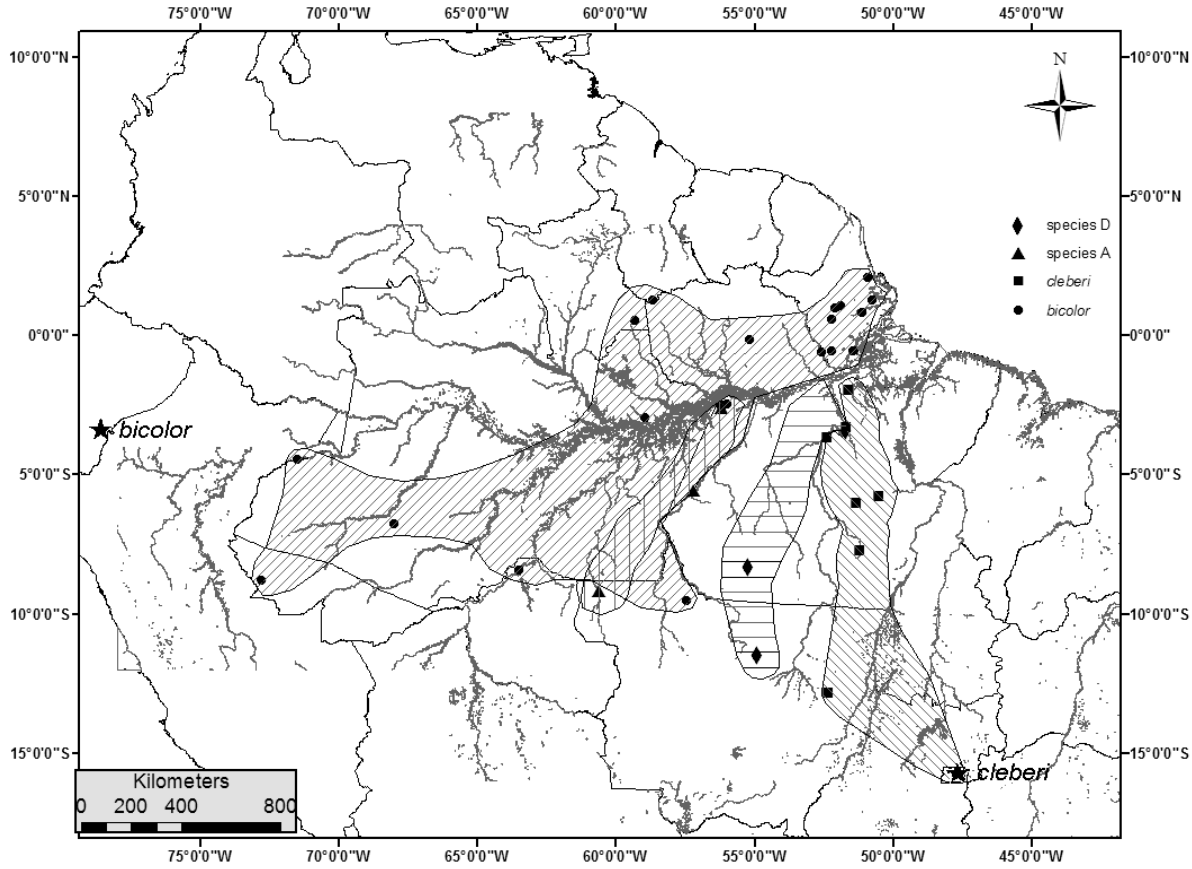

Figure 8 – Map of approximate distribution of *Oecomys bicolor* (solid circles), *O. cleberi* (solid squares), *Oecomys* sp. A (solid triangles) and *Oecomys* sp. D (solid diamonds); localities of analyzed specimens are plotted for each species, as well as the type locality for *O. bicolor* and *O. cleberi* (solid stars).

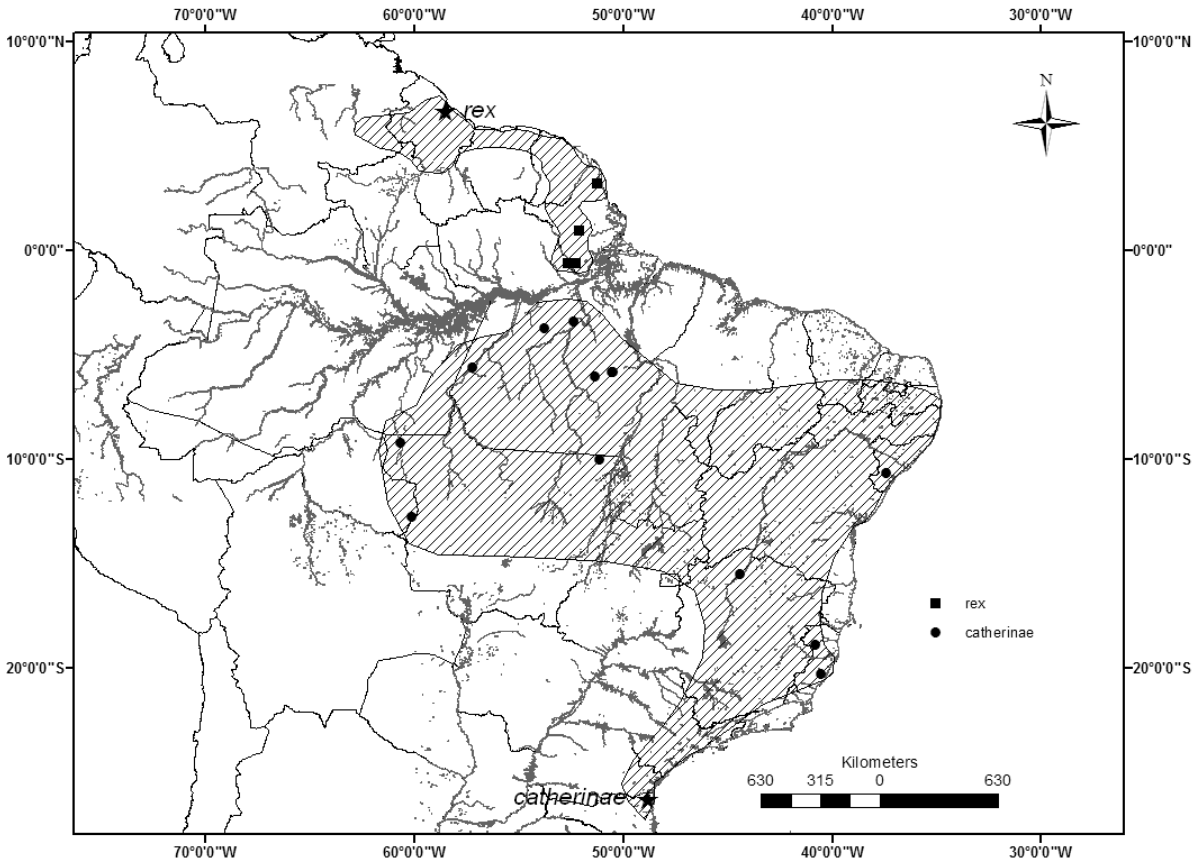

Figure 9 – Map of approximate distribution of *Oecomys catherinae* (solid circles) and *O. rex* (solid squares); localities of analyzed specimens are plotted for each species, as well as the type locality for both (solid stars).

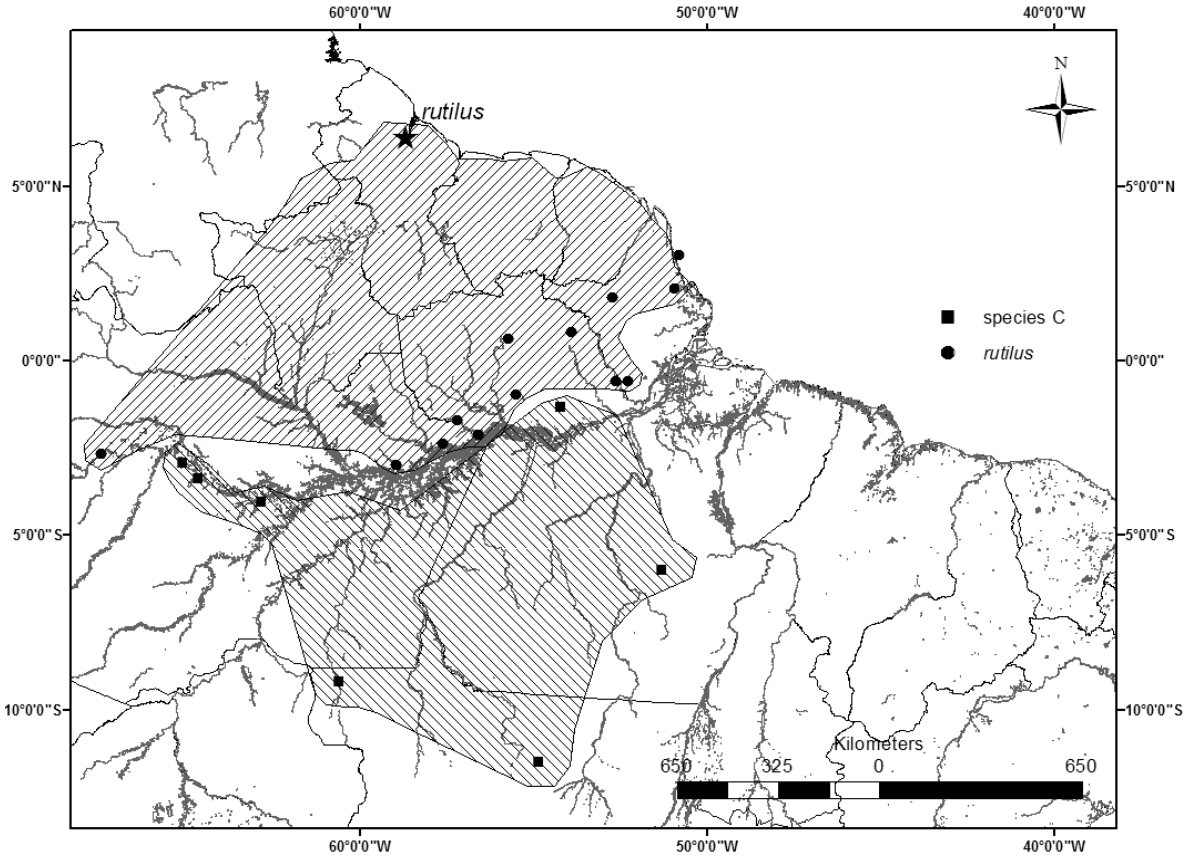

Figure 10 – Map of approximate distribution of *Oecomys rutilus* (solid circles) and *O.* species C (solid squares); localities of analyzed specimens are plotted for each species, as well as the type locality for *O. rutilus* (solid stars).

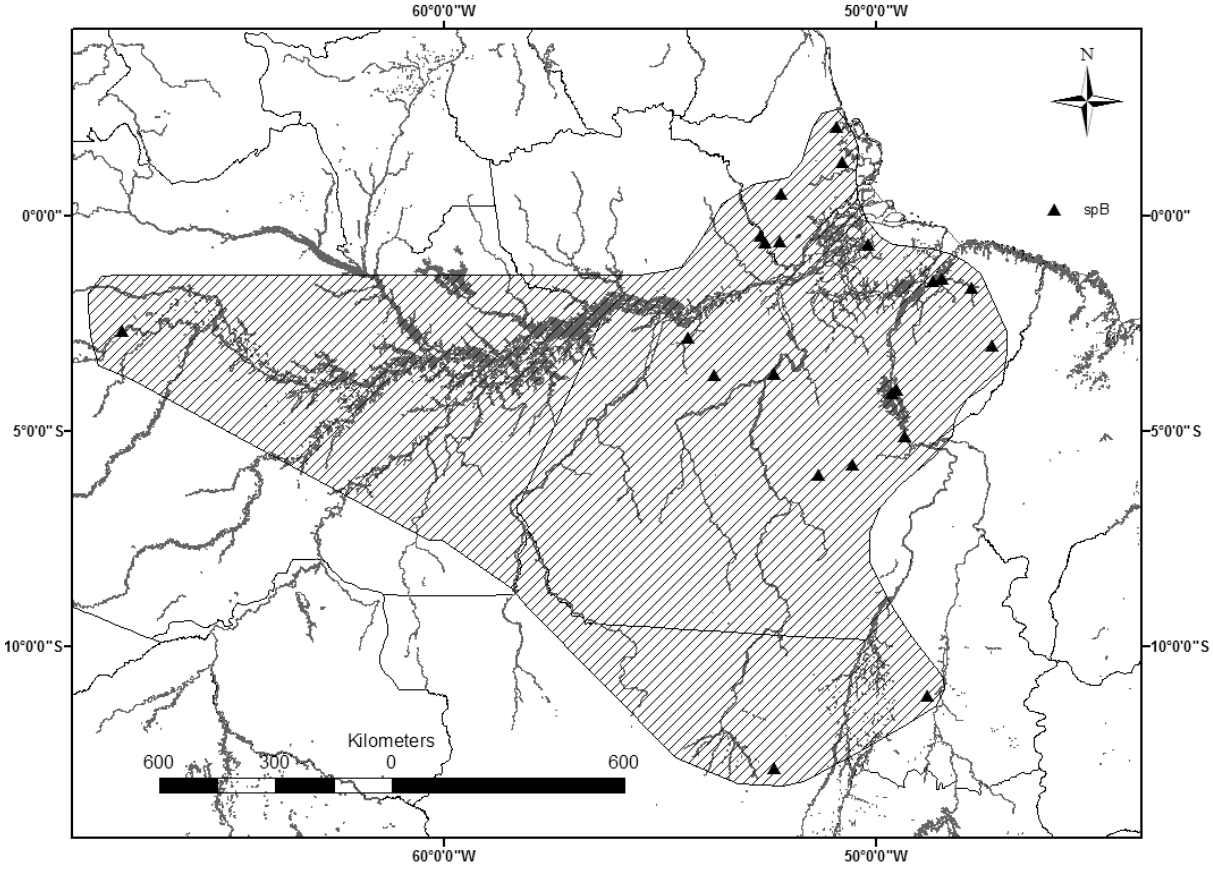

Figure 11 – Map of approximate distribution of *Oecomys* species B (solid triangles) with localities of analyzed specimens.

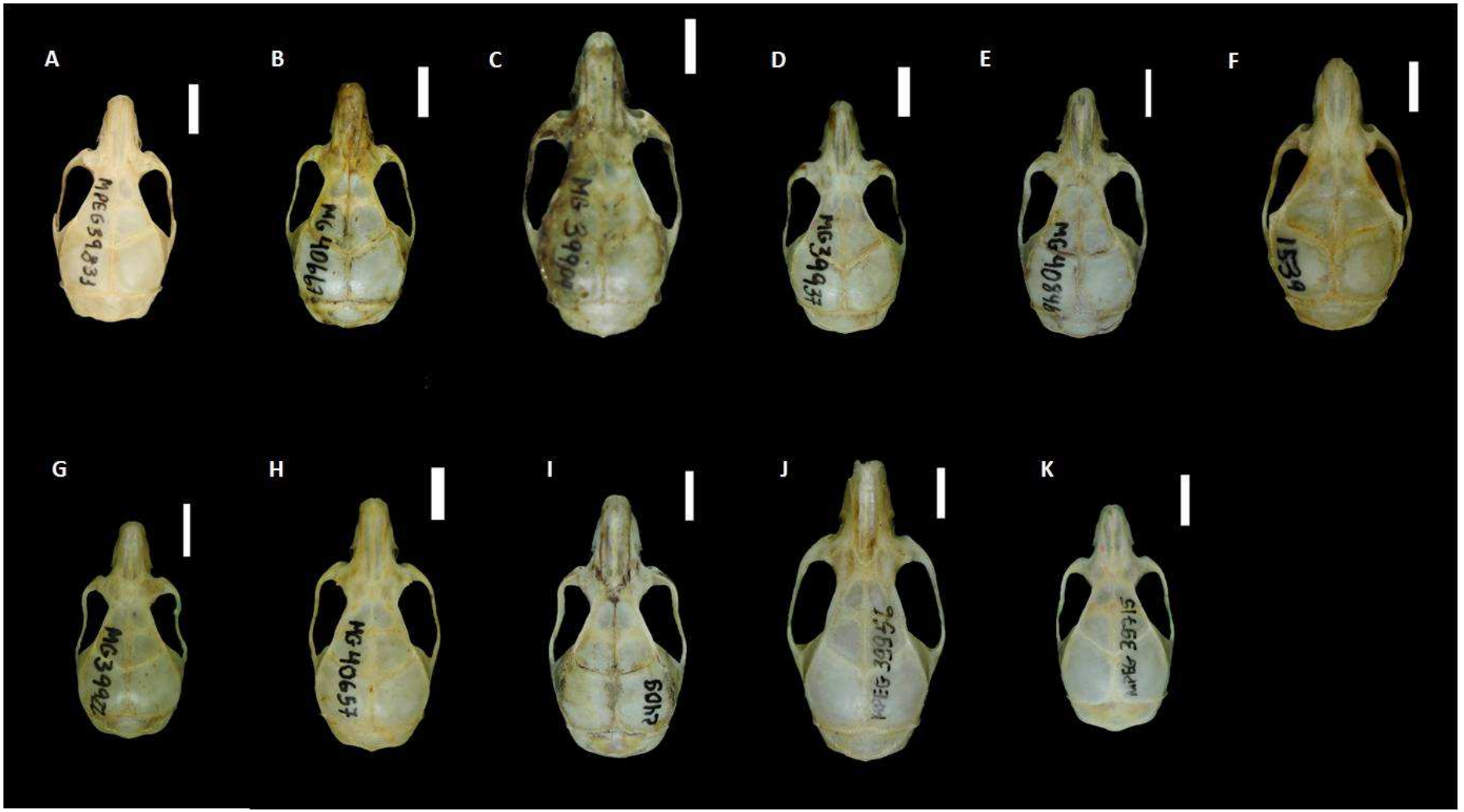

Figure 12 – Dorsal view of the skull of (**A**) *Oecomys auyantepui* (MPEG39831), (**B**) *O. bicolor* (MPEG40667), (**C**) *O. catherinae* (MPEG39909), (**D**) *O. cleberi* (MPEG39937), (**E**) *O. paricola* (MPEG40846), (**F**) *O. rex* (IEPA1539), (**G**) *O. rutilus* (MPEG39922), (**H**) *Oecomys* sp. A (MPEG40657), (**I**) *Oecomys* sp. B (IEPA2409), *Oecomys* sp. C (MPEG39956) and *Oecomys* sp. D (MPEG39715). Photos: Magno, R. & Flores, T., 2010.

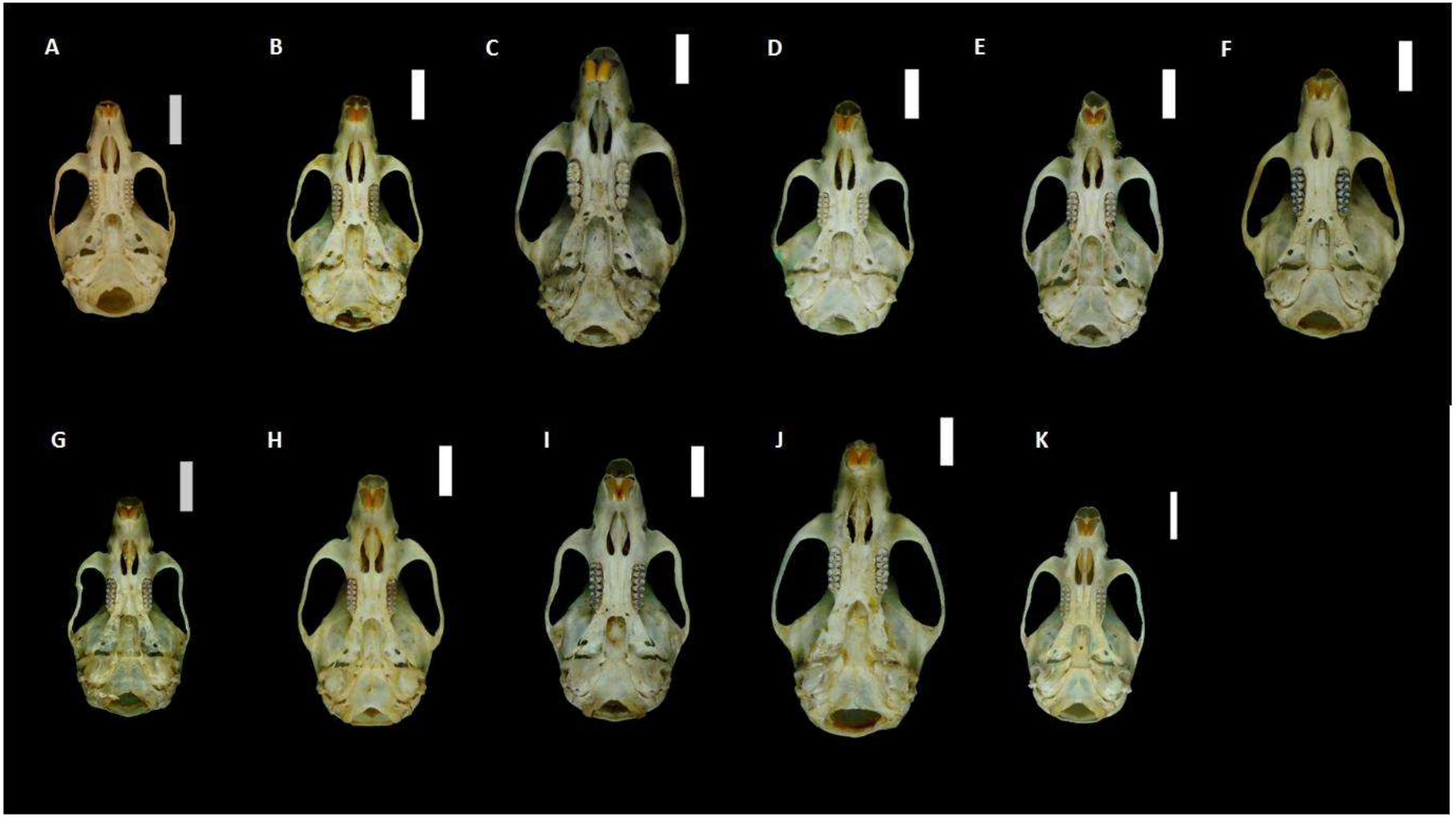

Figure 13 – Ventral view of the skull of (**A**) *Oecomys auyantepui* (MPEG39831), (**B**) *O. bicolor* (MPEG40667), (**C**) *O. catherinae* (MPEG39909), (**D**) *O. cleberi* (MPEG39937), (**E**) *O. paricola* (MPEG40846), (**F**) *O. rex* (IEPA1539), (**G**) *O. rutilus* (MPEG39922), (**H**) *Oecomys* sp. A (MPEG40657), (**I**) *Oecomys* sp. B (IEPA2409), *Oecomys* sp. C (MPEG39956) and *Oecomys* sp. D (MPEG39715). Photos: Magno, R. & Flores, T., 2010.

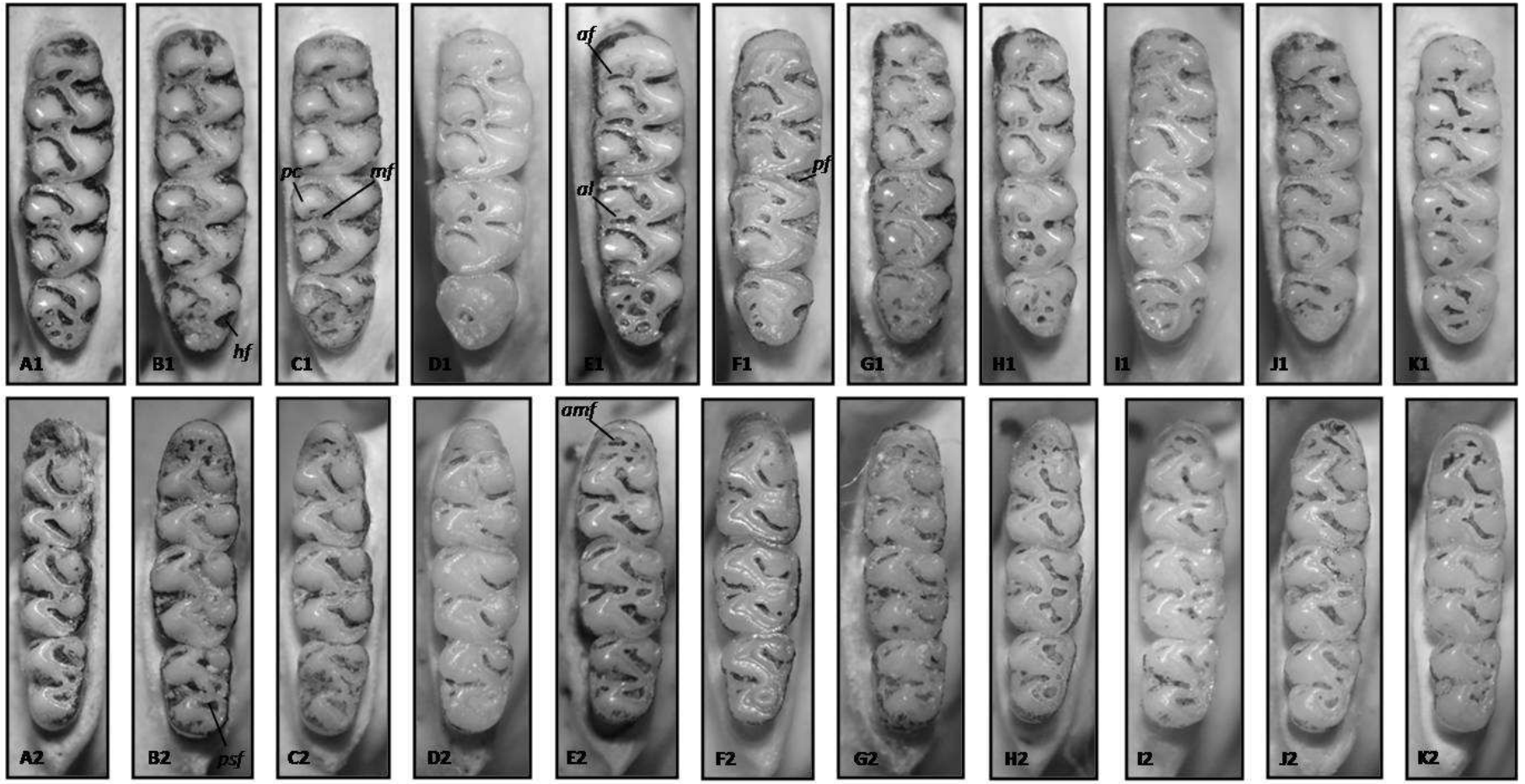

Figure 14 – Upper (**1**) and lower (**2**) molar rows of (**A**) *Oecomys rex* (IEPA1539), (**B**) *Oecomys* species C (IEPA2445), (**C**) *Oecomys* species B(IEPA2409), (**D**) *Oecomys catherinae* (MPEG12691), (**E**) *Oecomys auyantepui* (MPEG40448), (**F**) *Oecomys paricola* (MPEG39705), (**G**) *Oecomys bicolor* (MPEG40667), (**H**) *Oecomys* species A (MPEG40657), (**I**) *Oecomys cleberi* (MPEG39937), (**J**) *Oecomys rutilus* (MPEG39922) and (**K**) *Oecomys* species D (MPEG39715). Out of scale, but organized from the larger to the smaller. Legend: **af** – anteroflexus, **al** – accessory loph, **amf** – anteromedian fossettid, **hf** – hypoflexus, **mf** – mesoflexus, **pc** – paracone, **pf** – protoflexus, **psf** – posteroflexus. Photos: Flores, T., 2010.

TABLES

Table 1 – GenBank sequences used in our phylogenetic analysis.

Species	GenBank Entry	Locality
Oecomys bicolor	AF108699	[114] Peru[1] (Smith & Patton 1999)
Oecomys bicolor	OBU58382	[115] Brazil, Acre, Sobral, left bank Rio Juruá. 08º22'S 72º49'W (Patton & Da Silva 1995; Patton *et al.* 2000)
Oecomys roberti	ORU58384	[116] Brazil, Amazonas, Penedo, right bank Juruá. 06º50'S 70º45'W (Patton & Da Silva 1995; Patton *et al.* 2000)
Oecomys sp.[2]	AY072772	[117] Brazil, Mato Grosso do Sul, Corumbá. 19º00'S 57º36'W (Andrade & Bonvincino 2003)
Oecomys sp.	OSU58388	[118] Brazil, Amazonas, Lago Vai-Quem-Quer, right bank Rio Juruá. 03º19'S 66º01'W (Patton & Da Silva 1995; Patton *et al.* 2000)
Oecomys superans	AY275123	Not specified (D'Elia, 2003)
Oecomys superans	OSU58385	[116] Brazil, Amazonas, Penedo, right bank Juruá. 06º50'S 70º45'W (Patton & Da Silva 1995; Patton *et al.* 2000)
Oecomys trinitatis	OTU58390	[119] Brazil, Acre, Opposite Igarapé Porongaba, left bank Rio Juruá. 08º40'S 72º47'W (Patton & Da Silva 1995; Patton *et al.* 2000)
Hylaeamys megacephalus	AY275124	Not specified (D'Elia, 2003)

[1]There are two localities in Peru associated to two specimens of *Oecomys bicolor* in Smith & Patton (1999), but it is not clear from which one is the sequence available on GenBank.

[2]Probably *Oecomys mamorae*.

Table 2 - The number of base substitutions per site from averaging (evolutionary divergence) over all sequence pairs of cytochrome-*b* within each *Oecomys* species is shown below. All results are based on the pairwise analysis of 104 sequences with 653 base pairs including all codon positions. Standard error estimates are shown in the second column and were obtained by a bootstrap procedure (1000 replicates). The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.9321). The presence of n/c in the results denotes cases in which it was not possible to estimate evolutionary distances.

Species	Divergence (%)	Standard Error
Oecomys rex	1.1	0.3
Oecomys paricola	2.6	0.5
Oecomys sp.[1]	n/c	n/c
Oecomys auyantepui	1.6	0.2
Oecomys species B	3.0	0.5
Oecomys species C	3.9	0.8
Oecomys roberti[2]	n/c	n/c
Oecomys superans	2.6	0.6
Oecomys bicolor	2.7	0.4
Oecomys species D	2.0	0.5
Oecomys bicolor (Peru)[3]	n/c	n/c
Oecomys cleberi	1.0	0.3
Oecomys species A[4]	n/c	n/c
Oecomys species[5]	n/c	n/c
Oecomys species[6]	n/c	n/c
Oecomys trinitatis[7]	n/c	n/c
Oecomys catherinae	2.9	0.5
Oecomys rutilus	2.1	0.4

1 Specimen MZUSP29530 from Cláudia, Mato Grosso, Brazil; **2** *Oecomys roberti* from Rio Juruá (Patton *et al.* 2000; ORU58384); **3** *Oecomys bicolor* from Peru (Smith & Patton 1999; AF108699); **4** *Oecomys* sp.n. from Juruti, Pará (MPEG40657); **5** *Oecomys* sp. from Corumbá, Mato Grosso, Brazil (Andrade & Bonvincino 2003; AY072772), probably *O. mamorae*; **6** *Oecomys* sp. from Juruá River (Patton *et al.* 2000; OSU58388); **7** *Oecomys trinitatis* from Juruá River (Patton *et al.* 2000; OTU58390).

Table 3 - Estimates of evolutionary divergence over sequence pairs of cytochrome-*b* between *Oecomys* species are shown in lower part of table. All results are based on the pairwise analysis of 104 sequences with 653 base pairs including all codon positions. Standard error estimate(s) are shown in upper part of the table and were obtained by a bootstrap procedure (1000 replicates). The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.9321). All values are shown in percentages.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. *Oecomys rex*		1.6	1.7	1.5	1.7	1.7	1.5	1.6	1.7	1.7	1.8	1.9	1.8	1.8	1.7	1.8	1.3	1.6
2. *Oecomys paricola*	13.3		1.0	1.5	1.7	1.5	1.5	1.5	1.5	1.6	1.7	1.7	1.9	1.7	1.7	1.9	1.4	1.8
3. *Oecomys* sp.[1]	13.1	6.1		1.5	1.6	1.5	1.6	1.5	1.6	1.6	1.9	1.7	1.7	1.6	1.7	1.6	1.5	1.8
4. *Oecomys auyantepui*	12.4	12.2	11.7		1.8	1.7	1.8	1.9	1.7	1.7	1.9	1.7	2.1	1.7	1.8	1.9	1.5	1.6
5. *Oecomys* species B	13.7	13.8	12.1	14.9		1.0	1.1	1.3	1.2	1.2	1.3	1.4	1.5	1.4	1.4	1.5	1.5	1.6
6. *Oecomys* species C	13.5	12.3	12.0	13.6	7.1		1.0	1.3	1.3	1.3	1.4	1.5	1.6	1.4	1.5	1.5	1.5	1.7
7. *Oecomys roberti*[2]	12.4	12.7	12.3	13.8	7.6	6.7		1.2	1.3	1.3	1.4	1.5	1.5	1.6	1.6	1.7	1.6	1.9
8. *Oecomys superans*	12.1	11.4	10.5	14.9	10.3	10.2	8.7		1.3	1.3	1.5	1.5	1.6	1.6	1.5	1.7	1.6	1.7
9. *Oecomys bicolor*	13.9	11.7	11.7	14.0	9.5	10.4	10.3	9.7		0.9	1.1	1.0	1.4	1.4	1.3	1.7	1.4	1.7
10. *Oecomys* species D	14.0	13.3	12.7	14.3	8.9	10.5	10.0	9.9	6.2		1.1	1.1	1.4	1.4	1.3	1.7	1.5	1.6
11. *Oecomys bicolor*[3]	14.1	13.2	13.8	15.2	9.5	10.7	11.0	10.4	7.5	7.0		1.3	1.5	1.7	1.5	2.0	1.6	1.8
12. *Oecomys cleberi*	15.5	13.8	12.8	13.7	11.0	11.7	11.9	11.2	6.8	7.0	8.1		1.5	1.6	1.4	1.8	1.6	1.7
13. *Oecomys* species A[4]	14.4	14.1	12.3	16.1	11.4	12.0	12.2	11.3	10.2	9.7	10.6	10.0		1.6	1.4	1.7	1.7	1.9
14. *Oecomys* species[5]	13.9	12.9	11.1	13.6	10.2	10.0	11.8	11.9	10.1	10.6	11.0	11.3	10.9		1.3	1.7	1.7	1.8
15. *Oecomys* species[6]	14.2	12.9	11.7	13.6	10.7	11.5	12.0	11.6	9.1	9.4	10.9	10.0	9.7	8.9		1.8	1.5	1.7
16. *Oecomys trinitatis*[7]	13.7	15.0	12.2	15.9	12.0	12.0	12.9	12.7	13.3	13.5	14.6	13.5	12.3	12.3	13.1		1.9	2.0
17. *Oecomys catherinae*	9.6	11.5	11.6	12.2	13.2	12.9	13.2	12.7	11.7	12.8	12.5	12.7	13.5	12.8	11.9	15.3		1.6
18. *Oecomys rutilus*	13.6	15.4	13.9	13.2	13.7	13.8	15.7	13.2	13.1	13.3	14.1	12.8	15.0	13.7	13.0	17.0	13.3	

[1] Specimen MZUSP29530 from Cláudia, Mato Grosso, Brazil; **[2]** *Oecomys roberti* from Rio Juruá (Patton *et al.* 2000; ORU58384); **[3]** *Oecomys bicolor* from Peru (Smith & Patton 1999; AF108699); **[4]** *Oecomys* sp.n. from Juruti, Pará (MPEG40657); **[5]** *Oecomys* sp. from Corumbá, Mato Grosso, Brazil (Andrade & Bonvincino 2003; AY072772), probably *O. mamorae*; **[6]** *Oecomys* sp. from Juruá River (Patton *et al.* 2000; OSU58388); **[7]** *Oecomys trinitatis* from Juruá River (Patton *et al.* 2000; OTU58390).

Table 4 - Diagnostic external morphological comparisons among small to intermediate bodied species of *Oecomys* in eastern Brazilian Amazon.

	O. bicolor*	***O. cleberi***	***O. rutilus***	***Oecomys* sp. A**	***Oecomys* sp. D**
Known distribution	Guiana and western Tapajós River	Xingú and Cerrado (type locality)	Guiana	Rondônia	Tapajós
TL in relation to HBL	115 %	101 %	114 %	115 %	110 %
Scale triplets	Central hair longer and thicker (>2 scale rows) than lateral hairs	Same thickness; 3 scale rows (central), 2 scale rows (lateral); shorter in females	Central hair longer and thicker (> 2 scale rows) than lateral hairs	Same thickness; 3 scale rows (central), 2 scale rows (lateral); shorter in females	Central hair longer and thicker (> 3 scale rows) than lateral hairs
Tail color	Brown with ventral proximal part lighter	Dark brown	From dark brown to light brown	Blackish with sparsely white hairs	Dark brown
Caudal pencil	< 5 mm	< 5 mm	9 mm	9 mm	6.5 mm
Hindfoot	Broad; 15 % of HBL	Narrow; 21 % of HBL	Narrow; 23 % of HBL	Narrow; 23 % of HBL	Narrow; 23 % of HBL
Plantar surface	*Squamae* present	*Squamae* present	Smooth	Smooth	*Squamae* present
Color of ears	Brown in females and dark brown in males	From dark brown to light brown	Dark brown with cream base	Dark brown, lighter inside	Dark brown with orange hairs on inner surface
Maximum body fur length	6 mm	5.5 mm	8 mm	10 mm	4 mm (females), 6 mm (males)
Dorsal fur color	Bright brownish orange	Yellowish-brown	Yellowish to reddish brown	Dark reddish with bright reddish back parts	Orange-brownish; females are darker
Head fur color	Darker than dorsum	Same as dorsum	Same as dorsum	Dark reddish	Same as dorsum
Flank fur color	Lighter than dorsum	Lighter than dorsum with a bright yellow line	Lighter and grayish than dorsum	Lighter and brighter than dorsum	Brighter than dorsum
Ventral fur color	White to the roots with or w/o a thin line gray-based at sides of ventral surface	Vary from pure white to light gray-based; chin and throat are always white to the roots	White to the roots with a thin line of gray-based hairs at sides of ventral surfaces	White to the root with inner part of legs gray-based	White to the roots

* Species with geographical morphological variation discussed on text.

Table 5 - Diagnostic craniodental morphological comparisons among small to intermediate bodied species of *Oecomys* in eastern Brazilian Amazon.

	O. bicolor*	***O. cleberi***	***O. rutilus***	***Oecomys* sp. A**	***Oecomys* sp. D**
Nasal bone	Short	Short	Short	Long	Short
Supraorbital ridges	Slightly developed; generally extends to parietal bones	Slightly developed, almost absent	Slightly developed restricted to frontal bones	Slightly developed restricted to frontal bones	Slightly developed, almost absent
Mesopterygoid fossa	Never extends beyond maxillary bone	Never extends beyond maxillary bone	Extends beyond maxillary bone	Extends beyond maxillary bone	Generally do not extends beyond maxillary bone
Parapterygoid fossa roof	About the same level of palate bone	About the same level of palate bone; deeper in old specimens	Under palate level but above mesopterygoid fossa roof	Under palate level but above mesopterygoid fossa roof	About the same level of palate bone
Alisphenoid strut	Always absent	Always present	Often present	Present	Always absent
Anterior opening of alisphenoid canal	Large	Large	Small	Small	Large
Subsquamosal fenestra and process	Variable in size	The subsquamosal process is very thin and longer and the subsquamosal fenestra is always moderate in size	The subsquamosal process is thin and longer and the subsquamosal fenestra is always present and large	The subsquamosal process is thin and longer and the subsquamosal fenestra is always present and large	The subsquamosal process is very thin and longer and the subsquamosal fenestra is always moderate in size
Capsular process of lower incisor alveoli	Slightly curved	Slightly curved	Moderately curved	Accentuated curved	Slightly curved
Acessory root (M1)	Present	Present	Present	Absent	Absent
Accessory loph posterior to paracone in M2	Present	Variable	Present	Absent	Present
M3 hypoflexus	Shallow	Shallow	Deep	Shallow	Deep
m1 roots	3	2	2	2	2 or 3

* Species with geographical morphological variation discussed on text.

Table 6 – Diagnostic external morphological comparisons among intermediate to large bodied species of *Oecomys* in eastern Brazilian Amazon.

	O. auyantepui	***O. paricola****	***O. catherinae***	***O. rex***	***Oecomys* sp. B***	***Oecomys* sp. C**
Known distribution	Guiana	Belém, Xingú and Marajó	Atlantic Forest, Xingú, Tapajós and Rondônia	Guiana	Guiana, Belém and Xingú	Guiana and Rondônia
TL in relation to HBL	107 %	112 %	123 %	115 %	120 %	81 %
Scale triplets	Same thickness; almost 3 scale rows (central), 2 scale rows (lateral)	Same thickness; almost 3 scale rows (central), 2 scale rows (lateral)	Same thickness; 2 scale rows (central), $1^1/_2$ scale rows (lateral)	Central hair is thicker and longer (amost 2 scale rows) than lateral ones	Same thickness and length (almost 2 scale rows)	Same thickness; 2 scale rows (central), $1^1/_2$ scale rows (lateral)
Caudal pencil	5 – 8 mm	6.5 mm	Absent	Absent	Absent	Broken tail
Hindfoot	Small; 19 % of HBL	Narrow; 21 % of HBL	Broad; 22 % of HBL	Broad; 18 % of HBL	Broad; 22 % of HBL	Small; 16 % of HBL
Plantar surface	Smooth	Smooth	*Squamae* present	*Squamae* present	Smooth	Smooth
Metatarsal spot	Conspicuous only in olds	Present	Present	Absent	Absent	Absent
Maximum body fur length	11 mm	9 mm	13 mm	13 mm	9 mm	9 mm
Dorsal fur color	Yellow to reddish-brown	Dark yellowish-brown	Yellow-grayish	Dark yellow-grayish	Yellow to brown grayish	Dark yellowish-brown
Flank fur color	Distinctly lighter and grayish than dorsum	Lighter than dorsum	Slight lighter than dorsum	Lighter than dorsum	Lighter than dorsum	Lighter than dorsum with a bright orange line
Ventral fur color	Gray-based and cream-tipped or gray-based only on sides and pectoral region; chin and throat always pure cream	Grey-based and white-tipped; chin and throat pure white	Gray-based and white-tipped with a pure white spot in throat	Dark gray-based and white-tipped with a pure white spot in throat	Grey-based and white-tipped; chin and throat pure white	Gray-based with chin and throat pure white; inside legs and pectoral parts are lighter grayish than other ventral parts

* Species with geographical morphological variation discussed on text.

Table 7 - Diagnostic craniodental morphological comparisons among intermediate to large bodied species of *Oecomys* in eastern Brazilian Amazon.

	O. auyantepui	***O. paricola****	***O. catherinae***	***O. rex***	***Oecomys* sp. B***	***Oecomys* sp. C**
Nasal bone	Short	Long	Short	Short	Long	Long
Supraorbital ridges	Well developed slightly extends onto parietals border	Slightly developed restricted to frontals	Well developed, passing back as strongly marked ridges across the parietals	Much developed with a conspicuous postorbital horizontal process	Well developed restricted to frontals	Well developed restricted to frontals
Zygomatic notch	Shallow	Shallow	Distinct	Distinct	Shallow	Shallow
Mesopterygoid fossa	Extends beyond maxillary bone; totally ossified roof	Never extends beyond maxillary bone; totally ossified roof	Never extends beyond maxillary bone; totally ossified roof	Extends beyond maxillary bone; presence of spheno-palatines vacuities	Never extends beyond maxillary bone; totally ossified roof	Extends beyond maxillary bone; totally ossified roof
Alisphenoid strut	Present at least on one side	Always absent	Always absent	Always absent	Always absent	Always absent
Anterior opening of alisphenoid canal	Always absent	Always present	Always present and large	Always present and large	Always present but small	Always present but small
Subsquamosal fenestra	Always absent	Always present	Always present but small	Always present but small	Always present	Always present
Position of mental foramen	Lateral	Lateral	Frontal	Frontal	Lateral	Lateral
Capsular process of lower incisor alveoli	Moderatly curved	Slightly curved	Strongly curved	Slightly curved	Slightly curved	Slightly curved
Accessory root (M1)	Absent	Absent	Present	Absent	Absent	Absent
M2 protoflexus	Present	Present	Absent	Absent	Present	Present
m1 roots	2	2	3	2	2	2

* Species with geographical morphological variation discussed on text.

Table 8 – Selected external and cranial dimensions for three small to intermediate bodied *Oecomys* species from eastern Brazilian Amazon. Measurements (mm) are given as mean ± standart error, with range and sample size. Individuals of all localities were grouped together.

	O. bicolor			***O. cleberi***			***O. rutilus***		
Variable	Mean±SE	Range	n	Mean±SE	Range	n	Mean±SE	Range	n
Sex	17 females, 35 males, 3 unk.			8 females, 5 males			8 females, 11 males, 2 unk.		
HBLL	99.0±14.7	75.0 – 140.0	38	92.2±7.3	83.0 – 103.0	13	82.9±9.8	66.0 – 98.0	16
TL	103.0±18.7	50.0 – 150.0	39	93.5±8.1	80.0 – 108.0	13	93.8±10.2	70.0 – 110.0	16
FL	20.8±2.0	16.0 – 26.0	39	19.3±1.5	16.0 – 21.0	12	19.1±2.5	13.0 – 23.0	15
EL	13.3±2.0	7.0 – 18.0	39	13.2±1.3	10.0 – 15.0	13	12.9±1.9	8.0 – 17.0	15
CIL	23.5±1.9	19.1 – 29.7	52	22.5±1.1	21.0 – 24.1	12	21.5±1.7	18.2 – 25.1	21
BH	7.7±0.4	6.7 – 8.5	49	7.5±0.3	7.1 – 7.9	12	7.5±0.4	6.8 – 8.2	21
CZL	18.9±1.4	15.7 – 23.7	51	18.1±0.9	16.9 – 19.4	12	17.2±1.5	14.6 – 20.4	21
ZL	11.8±1.0	9.9 – 15.3	54	11.1±0.6	10.4 – 11.9	13	10.7±0.9	9.2 – 12.8	21
BZP	2.2±0.3	1.7 – 3.4	54	2.0±0.3	1.6 – 2.4	13	2.0±0.3	1.5 – 2.7	21
LD	6.7±0.6	5.6 – 8.6	54	6.3±0.3	5.6 – 6.8	13	6.1±0.6	4.9 – 7.2	21
BI	1.5±0.2	1.1 – 1.8	53	1.4±0.2	1.2 – 1.7	13	1.4±0.1	1.0 – 1.6	21
LN	8.8±0.9	7.3 – 11.1	51	8.5±0.6	7.7 – 9.9	11	8.0±0.9	6.5 – 10.0	20
RL	8.7±0.8	7.3 – 11.5	51	8.2±0.5	7.3 – 9.1	11	7.8±0.8	6.0 – 9.3	20
RB	3.4±0.2	3.0 – 4.1	51	3.2±0.1	3.0 – 3.4	13	3.2±0.2	2.9 – 3.7	21
OL	9.3±0.7	7.7 – 11.6	54	8.9±0.4	8.3 – 9.5	13	8.5±0.6	7.3 – 10.2	21
LIB	4.8±0.3	4.2 – 5.9	55	4.6±0.2	4.4 – 5.0	13	4.5±0.3	4.0 – 5.1	21
ZB	13.7±0.9	11.9 – 15.8	52	13.1±0.7	12.0 – 14.0	11	12.6±1.0	10.7 – 14.7	20
BIP	8.9±0.6	7.7 – 10.1	52	8.9±0.4	8.1 – 9.5	12	8.7±0.5	7.7 – 9.6	21
LIP	3.7±0.5	2.5 – 5.4	52	3.5±0.3	3.0 – 4.0	12	3.7±0.3	2.8 – 4.2	21
MB	10.0±0.4	9.3 – 11.1	49	9.8±0.2	9.3 – 10.2	12	9.5±0.4	8.8 – 10.4	20
BPR	4.0±0.3	3.3 – 4.8	52	3.9±0.2	3.6 – 4.2	13	3.8±0.3	3.3 – 4.3	21
BIF	2.1±0.2	1.6 – 2.9	54	2.0±0.1	1.9 – 2.2	13	2.0±0.1	1.8 – 2.4	21
LIF	4.4±0.4	3.6 – 5.5	54	4.3±0.2	4.0 – 4.7	13	4.0±0.4	3.4 – 5.2	21
LM	3.8±0.2	3.1 – 4.7	54	3.6±0.1	3.5 – 3.7	13	3.4±0.2	3.1 – 3.9	20
BM1	1.0±0.1	0.9 – 1.3	54	1.0±0.0	0.9 – 1.1	13	0.9±0.1	0.8 – 1.1	21
BPB	2.7±0.2	2.2 – 3.1	52	2.6±0.2	2.3 – 2.8	13	2.5±0.2	2.0 – 3.0	21
LPB	4.6±0.5	4.0 – 6.6	50	4.3±0.2	4.0 – 4.6	13	4.2±0.3	3.8 – 4.7	21
BB	4.2±0.2	3.7 – 4.8	48	4.2±0.1	4.1 – 4.5	11	4.0±0.2	3.5 – 4.4	20
OCB	6.0±0.3	5.5 – 7.2	48	5.9±0.2	5.6 – 6.2	12	5.7±0.2	5.2 – 6.3	21
LLD	3.5±0.3	3.0 – 4.5	51	3.4±0.2	3.1 – 3.6	13	3.2±0.3	2.6 – 3.7	18
Bm1	0.9±0.1	0.8 – 1.2	51	0.9±0.1	0.8 – 1.0	13	0.8±0.1	0.8 – 1.0	18
LLM	4.0±0.2	3.4 – 5.0	51	3.8±0.1	3.5 – 3.9	13	3.6±0.3	3.3 – 4.1	17
MH	6.1±0.6	5.2 – 7.8	51	6.0±0.3	5.4 – 6.5	13	5.7±0.6	4.7 – 7.1	18
LCIB	14.0±1.2	11.6 – 18.4	51	13.6±0.4	12.8 – 14.1	13	12.9±1.0	11.0 – 14.7	18

Table 9 – Selected external and cranial dimensions for four intermediate to large bodied *Oecomys* species from eastern Brazilian Amazon. Measurements (mm) are given as mean ± standart error, with range and sample size. Individuals of all localities were grouped together.

	O. auyantepui			***O. paricola***			***O. catherinae***			***O. rex***		
Variable	Mean±SE	Range	n	Mean±SE	Range	n	Mean±SE	Range	n	Mean±SE	Range	n
Sex	16 females, 35 males			36 females, 63 males, 31 unk.			9 females, 5 males, 2 unk.			3 males, 2 unk.		
HBLL	102.5±10.4	79 – 120	43	103.4±11.6	76.0 – 129.0	91	123.8±18.6	77.0 – 146.0	10	123.5±29.0	103.0 – 144.0	2
TL	107.4±13.0	77 – 132	38	118.9±13.2	80.0 – 150.0	91	142.5±21.0	85.0 – 155.0	10	137.0±1.4	136.0 – 138.0	2
FL	21.3±2.1	14 – 25	42	22.6±1.7	18.0 – 29.0	91	25.9±2.9	19.0 – 155.0	10	22.0±8.5	16.0 – 28.0	2
EL	15.1±3.0	7 – 27	44	14.8±1.4	12.0 – 19.0	91	15.4±2.5	11.0 – 29.0	10	20.0±2.8	18.0 – 22.0	2
CIL	24.4±1.7	20.9 – 27.2	49	25.4±1.6	21.1 – 28.6	124	29.2±1.3	27.0 – 19.0	15	28.0±3.3	24.4 – 32.1	4
BH	7.9±0.4	6.9 – 8.6	47	7.9±0.4	6.7 – 8.8	125	8.5±0.3	8.0 – 31.1	16	8.5±0.5	8.0 – 9.1	4
CZL	19.5±1.3	17.0 – 21.7	49	20.2±1.5	13.3 – 22.7	124	23.4±1.1	21.8 – 9.1	15	22.6±2.8	19.6 – 26.0	4
ZL	12.2±0.9	10.7 – 13.6	51	12.8±1.2	2.6 – 14.6	129	15.2±0.8	13.7 – 24.9	15	15.1±1.8	13.5 – 17.5	4
BZP	2.3±0.3	1.8 – 2.8	51	2.5±0.6	1.5 – 8.0	130	3.5±0.2	3.0 – 16.3	16	3.3±0.5	2.6 – 3.9	5
LD	7.2±0.6	5.9 – 8.4	50	7.3±0.8	1.7 – 8.5	129	8.1±0.5	7.1 – 3.7	16	8.2±1.1	6.7 – 9.4	5
BI	1.5±0.2	1.1 – 2.0	50	1.6±0.8	1.1 – 10.3	127	1.9±0.2	1.6 – 8.8	15	1.9±0.2	1.5 – 2.1	5
LN	8.9±0.8	7.6 – 10.3	44	9.5±0.7	7.6 – 10.9	122	11.2±0.4	10.5 – 12.0	15	11.1±1.0	10.0 – 11.9	3
RL	8.7±0.7	7.3 – 9.9	44	9.3±0.7	7.5 – 10.6	122	11.3±0.5	10.6 – 12.6	15	11.0±1.1	9.7 – 11.7	3
RB	3.5±0.2	2.9 – 3.8	49	3.7±0.2	3.2 – 4.3	128	4.1±0.3	3.8 – 4.8	16	4.0±0.2	3.9 – 4.4	5
OL	9.6±0.6	8.3 – 10.6	51	10.0±0.5	8.3 – 11.2	129	11.5±0.5	10.6 – 12.3	15	11.5±1.0	10.5 – 12.8	4
LIB	5.2±0.3	4.4 – 5.8	51	5.1±0.3	4.5 – 5.7	129	5.4±0.4	4.8 – 6.5	15	6.2±0.3	5.9 – 6.6	5
ZB	14.3±1.0	12.6 – 16.2	50	14.6±1.0	11.6 – 16.7	124	16.6±0.8	15.3 – 17.7	14	16.4±1.7	14.7 – 18.1	3
BIP	9.4±0.5	8.0 – 10.6	48	9.1±0.5	8.1 – 10.4	127	9.5±0.6	8.3 – 11.0	16	9.9±0.4	9.2 – 10.3	4
LIP	3.7±0.3	3.1 – 4.5	48	4.0±0.4	2.9 – 5.0	128	4.3±0.6	3.2 – 5.5	16	4.8±0.3	4.6 – 5.2	4
MB	10.1±0.9	4.2 – 10.9	48	10.2±0.6	4.7 – 11.1	122	10.5±1.5	5.3 – 11.4	15	10.8±0.7	10.0 – 11.6	4
BPR	4.1±0.4	2.3 – 4.8	51	4.3±0.4	2.5 – 5.1	129	4.8±0.7	2.3 – 5.5	16	4.8±0.4	4.1 – 5.0	5
BIF	2.3±0.4	1.9 – 4.8	51	2.3±0.3	1.8 – 5.5	128	2.7±0.7	2.1 – 4.9	16	2.5±0.4	2.2 – 2.9	5
LIF	4.5±0.3	3.6 – 5.1	50	4.7±0.4	3.8 – 5.5	130	5.3±0.3	4.6 – 5.8	16	5.4±0.8	4.3 – 6.3	5
LM	3.9±0.2	3.6 – 4.4	50	4.2±0.3	1.2 – 5.1	130	4.7±0.9	1.5 – 5.2	16	5.3±0.2	5.0 – 5.6	5
BM1	1.1±0.1	1.0 – 1.3	50	1.2±0.1	1.0 – 1.4	129	1.5±0.5	1.3 – 3.3	16	1.5±0.1	1.5 – 1.6	5
BPB	2.8±0.4	2.4 – 4.9	49	2.9±0.3	2.3 – 5.8	127	3.4±1.0	2.7 – 6.9	15	3.0±0.3	2.6 – 3.4	5
LPB	5.2±0.6	2.1 – 6.3	51	5.3±0.4	2.0 – 6.2	127	6.1±1.1	2.3 – 7.2	15	6.4±0.4	5.7 – 6.7	5
BB	4.3±0.3	3.8 – 6.2	48	4.4±0.3	3.9 – 6.6	126	4.9±0.6	4.4 – 6.8	14	5.0±0.3	4.6 – 5.3	5
OCB	6.1±0.4	3.9 – 6.6	50	6.2±0.3	4.0 – 6.9	119	6.5±0.7	4.2 – 7.1	14	6.5±0.2	6.4 – 6.8	4
LLD	3.6±0.5	1.1 – 4.5	49	3.7±0.4	1.1 – 4.7	112	3.7±0.8	1.3 – 4.5	15	3.9±0.5	3.4 – 4.5	5
Bm1	1.1±0.5	0.9 – 4.2	48	1.0±0.3	0.8 – 4.4	113	1.4±1.0	1.1 – 5.2	16	1.3±0.0	1.3 – 1.4	5
LLM	4.1±0.3	3.8 – 6.1	49	4.3±0.4	3.5 – 7.6	112	5.3±1.0	4.7 – 8.7	15	5.4±0.2	5.1 – 5.7	5
MH	6.7±1.0	5.5 – 12.2	50	7.0±1.0	5.4 – 15.1	109	8.9±2.5	6.9 – 17.2	14	8.2±1.0	6.7 – 9.5	5
LCIB	14.7±1.1	10.4 – 16.8	50	15.2±1.1	11.8 – 17.5	113	17.4±1.0	14.2 – 18.6	16	17.2±1.4	15.3 – 18.7	5

Table 10 – Selected external and cranial dimensions for *Oecomys* new species from eastern Brazilian Amazon. Measurements (mm) are given as mean ± standart error, with range and sample size. Individuals of all localities were grouped together.

	***Oecomys* sp. A**			***Oecomys* sp. B**			***Oecomys* sp. C**			***Oecomys* sp. D**		
Variable	Mean±SE	Range	n	Mean±SE	Range	n	Mean±SE	Range	n	Mean±SE	Range	n
Sex	1 female, 1 male			21 females, 19 males, 3 unk.			3 females, 2 males			3 females, 3 males		
HBLL	101.5±2.1	100.0 – 103.0	2	120.0±14.5	89.0 – 142.0	30	126.0±6.7	120.0 – 135.0	4	95.2±39.9	62.0 – 174.0	6
TL	94.0±33.9	70.0 – 118.0	2	142.0±18.9	95.0 – 171.0	30	132.8±21.1	103.0 – 150.0	4	76.6±14.5	52.0 – 86.0	6
FL	22.0±2.8	20.0 – 24.0	2	25.8±2.9	17.0 – 30.0	30	23.8±3.0	20.0 – 27.0	4	17.3±4.0	12.0 – 20.5	6
EL	14.0±5.7	10.0 – 18.0	2	15.7±3.3	11.0 – 28.0	30	16.0±3.6	11.0 – 19.0	4	12.3±1.6	10.5 – 15.0	6
CIL	24.9±0.8	24.3 – 25.4	2	28.4±1.9	24.2 – 31.3	40	28.1±1.0	26.6 – 29.0	4	21.1±2.1	18.3 – 24.6	6
BH	8.1±0.4	7.8 – 8.4	2	8.4±0.5	7.0 – 9.7	41	8.4±0.3	8.0 – 8.8	5	7.1±0.3	6.5 – 7.5	6
CZL	19.6±0.7	19.1 – 20.1	2	22.7±1.5	19.1 – 24.7	40	22.6±0.9	21.3 – 23.2	4	17.1±1.8	14.9 – 20.0	6
ZL	12.3±0.8	11.8 – 12.8	2	14.5±1.0	12.4 – 16.2	43	15.0±0.6	14.2 – 15.5	5	10.5±1.0	9.3 – 12.2	6
BZP	2.2±0.1	2.2 – 2.2	2	3.0±0.3	2.5 – 3.7	43	3.1±0.3	2.7 – 3.4	5	1.9±0.3	1.5 – 2.3	6
LD	7.3±0.4	7.0 – 7.6	2	8.1±0.6	7.0 – 9.1	43	8.3±0.6	7.7 – 9.1	5	5.8±0.7	4.9 – 6.9	6
BI	1.7±0.0	1.7 – 1.7	2	1.7±0.2	1.4 – 2.1	42	1.8±0.2	1.5 – 1.9	4	1.3±0.1	1.1 – 1.5	6
LN	9.3±0.3	9.1 – 9.6	2	11.5±1.1	9.4 – 13.5	41	11.2±0.1	11.1 – 11.3	4	7.9±1.0	6.8 – 9.5	5
RL	8.9±0.2	8.7 – 9.0	2	10.9±0.9	9.0 – 12.5	41	10.8±0.6	9.9 – 11.3	4	7.3±1.0	6.3 – 9.0	5
RB	3.6±0.2	3.4 – 3.7	2	4.2±0.4	3.4 – 5.1	43	4.2±0.2	3.9 – 4.4	5	3.1±0.2	2.8 – 3.4	6
OL	10.0±0.3	9.8 – 10.3	2	11.1±0.6	9.6 – 12.3	43	11.3±0.4	10.8 – 11.9	5	8.5±0.8	7.5 – 9.9	6
LIB	5.1±0.4	4.7 – 5.4	2	5.4±0.4	4.7 – 6.7	43	5.6±0.2	5.4 – 6.0	5	4.3±0.2	3.9 – 4.5	6
ZB	14.6	-	1	16.3±1.3	13.4 – 18.3	41	16.6±0.7	15.8 – 17.6	4	12.5±1.2	11.3 – 14.6	6
BIP	9.3±0.2	9.2 – 9.4	2	8.9±0.8	7.4 – 10.7	43	9.0±0.5	8.4 – 9.7	5	8.7±0.4	8.3 – 9.3	6
LIP	3.8±0.3	3.7 – 4.0	2	4.2±0.6	3.0 – 5.5	43	4.2±0.4	3.7 – 4.7	4	3.9±0.4	3.4 – 4.3	6
MB	10.2±0.2	10.0 – 10.3	2	10.9±0.5	9.8 – 11.8	39	9.6±2.8	4.7 – 11.3	5	9.4±0.4	8.9 – 10.0	6
BPR	4.3±0.1	4.2 – 4.3	2	4.9±0.4	4.1 – 5.6	43	4.5±1.1	2.6 – 5.3	5	3.7±0.3	3.3 – 4.1	6
BIF	2.4±0.0	2.4 – 2.4	2	2.6±0.3	2.0 – 3.2	43	3.0±1.2	2.2 – 5.2	5	1.8±0.1	1.6 – 1.9	6
LIF	4.7±0.3	4.5 – 5.0	2	5.2±0.5	4.3 – 6.2	43	5.1±0.4	4.7 – 5.7	5	4.0±0.4	3.3 – 4.4	6
LM	3.8±0.1	3.7 – 3.8	2	4.8±0.2	4.1 – 5.2	43	4.2±1.6	1.4 – 5.0	5	3.4±0.1	3.3 – 3.5	6
BM1	1.0±0.0	1.0 – 1.1	2	1.3±0.1	1.1 – 1.5	43	1.8±0.9	1.3 – 3.5	5	0.9±0.0	0.9 – 1.0	6
BPB	2.9±0.0	2.9 – 2.9	2	3.1±0.3	2.4 – 3.7	42	3.7±1.4	2.8 – 6.2	5	2.4±0.3	2.1 – 2.9	6
LPB	4.6±0.3	4.4 – 4.8	2	6.2±0.5	5.1 – 7.2	43	5.5±1.8	2.2 – 6.7	5	4.1±0.3	3.6 – 4.6	6
BB	4.4±0.2	4.3 – 4.5	2	4.6±0.2	4.2 – 5.3	41	5.0±1.1	4.1 – 6.8	5	4.0±0.2	3.7 – 4.3	6
OCB	6.1±0.2	6.0 – 6.3	2	6.7±0.3	5.9 – 7.2	38	5.9±1.4	3.8 – 6.9	4	5.5±0.2	5.3 – 5.7	6
LLD	3.8±0.0	3.8 – 3.8	2	4.1±0.3	3.4 – 4.7	41	3.6±1.4	1.2 – 4.7	5	3.0±0.3	2.8 – 3.6	6
Bm1	0.9±0.1	0.9 – 1.0	2	1.1±0.1	0.8 – 1.2	42	1.9±1.7	1.2 – 4.9	5	0.8±0.0	0.7 – 0.9	6
LLM	4.0±0.1	3.9 – 4.1	2	5.0±0.2	4.2 – 5.4	40	5.5±1.2	5.0 – 7.7	5	3.6±0.1	3.5 – 3.7	6
MH	6.6±0.2	6.5 – 6.7	2	7.7±0.7	6.1 – 9.0	38	9.3±3.4	7.4 – 15.4	5	5.5±0.6	5.0 – 6.6	6
LCIB	14.6±0.9	14.0 – 15.3	2	17.1±1.2	14.5 – 19.5	42	16.4±2.4	12.4 – 18.4	5	12.6±1.0	11.7 – 14.5	6

Table 11 - Standardized discriminant coefficients for canonical variables for the first two axes (DF) in comparisons among (**A**) all species from eastern Brazilian Amazon, (**B**) the four larger species (*Oecomys catherinae*, *O. rex*, *O.* species B and *O.* species C), and (**C**) the remaining smaller species (*Oecomys auyantepui*, *O. bicolor*, *O. cleberi*, *O. paricola*, *O. rutilus*, *O.* species A and *O.* species D), based on 16 log10 cranial variables.

	A		**B**		**C**	
Variable	DF-1	DF-2	DF-1	DF-2	DF-1	DF-2
Log BZP	-0.29004	0.08973	0.55847	-0.87439	0.030712	-0.130897
Log LN	-0.08074	0.48848	-1.48280	-0.01191	0.097101	-0.264857
Log RB	-0.23464	0.51781	0.01727	0.62215	-0.059730	-0.703942
Log LIB	0.20175	-0.63662	-0.31589	0.84190	-0.061293	0.855142
Log BIP	0.11800	-0.34015	-0.29873	-0.48468	-0.021199	0.201832
Log LIP	0.04122	0.26855	0.54687	0.27228	0.256105	-0.311012
Log MB	-0.02260	0.10809	0.48075	0.05375	0.197387	0.946173
Log BIF	-0.00379	-0.18304	0.15289	-0.17563	-0.160378	-0.302695
Log LM	-0.37233	0.00017	2.44376	1.53467	-0.089446	-0.128230
Log BM1	-0.31974	-0.26545	1.41378	1.38452	-0.360944	-0.003919
Log BPB	0.15599	-0.03225	0.21493	-0.48458	0.021019	0.328454
Log LPB	-0.32709	-1.04467	0.24844	-0.27772	-0.905159	0.258373
Log BB	0.13920	0.38773	1.19467	0.66240	0.355308	-0.588776
Log OCB	0.21802	-0.02881	-0.27944	-1.34018	0.099631	-0.207676
Log Bm1	0.35380	-1.53507	0.70252	0.06569	-0.380273	2.129593
Log LLM	-1.02681	0.70347	-0.36019	-1.60705	-0.430337	-0.998183
Eingenvalue	6.27299	1.14076	2.25098	0.73570	2.492147	1.282191
% contribution	73.643	13.392	64.124	20.958	58.0652	29.8742