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DIVERSIDADE DE ESPÉCIES NO COMPLEXO *MONODELPHIS BREVICAUDATA* (DIDELPHIMORPHIA: DIDELPHIDAE), INFERIDA POR DADOS MOLECULARES E MORFOLÓGICOS

SILVIA ELIZA D`OLIVEIRA PAVAN

BELÉM, PARÁ

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

> **Orientador: Rogério Vieira Rossi**

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MUSEU PARAENSE EMÍLIO GOELDI
UNIVERSIDADE FEDERAL DO PARÁ
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA
CURSO DE MESTRADO EM ZOOLOGIA

DIVERSIDADE DE ESPÉCIES NO COMPLEXO *MONODELPHIS BREVICAUDATA* ERXLEBEN, 1777 (DIDELPHIMORPHIA: DIDELPHIDAE), INFERIDA POR DADOS MOLECULARES (CIT B, 16 S) E MORFOLÓGICOS

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"Há uma grandeza nesta visão da vida, com seus vários poderes, ter sido inspirada originalmente em umas poucas formas, ou em uma só; e isso, enquanto este planeta vai executando seus ciclos de acordo com a lei imutável da gravidade; de um começo tão simples foram, e estão sendo, produzidas formas sem fim, as mais belas e mais maravilhosas."

Charles Darwin (1809 – 1882)

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AGRADECIMENTOS

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SUMÁRIO

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RESUMO

O complexo de espécies *M. brevicaudata* possui distribuição reconhecida para o Norte da América do sul e compreende três espécies descritas - *M. brevicaudata, M. glirina*, e *M. palliolata* - e duas não descritas, reconhecidas em estudos prévios. A delimitação de espécies baseada somente em caracteres morfológicos é complicada, de forma que diversos táxons nominais já foram associados ao grupo e diversos arranjos taxonômicos foram propostos. Os poucos estudos baseados em dados moleculares que incluíram espécimes do complexo *brevicaudata* revelaram altas taxas de divergência genética. Este trabalho buscou elucidar a sistemática do complexo de espécies *M. brevicaudata* através do estudo dos padrões de variação morfológica e genética. Para tal, desenvolvemos análises filogenéticas baseadas em dois genes mitocondriais: citocromo b e 16 S rDNA. Adicionalmente, estudamos a morfologia externa e craniana dos espécimes, investigando a existência de congruência entre a variação genética e morfológica. As análises morfológicas foram, em geral, congruentes com as moleculares, as quais indicaram os mesmos clados em todas as análises filogenéticas. Foram formalmente reconhecidas nove espécies para o complexo. *Monodelphis brevicaudata*, *M. palliolata* e *M. glirina* são consideradas espécies válidas; *M. touan* é revalidado da sinonímia de *M. brevicaudata* e duas espécies novas são descritas e nomeadas; a espécie *M. domestica* provou ser intimamente relacionada a espécimes do grupo *brevicaudata*, sendo aqui considerada como integrante do referido grupo; duas espécies reconhecidas como distintas permanecem sem uma descrição formal; *M. maraxina* é sinonimizada com *M. glirina*. Foi observado dimorfismo sexual para as espécies estudadas, sendo que para as duas espécies estatisticamente testadas (teste T de student), *M. glirina* e *M*. sp. nov. "Trombetas", os machos apresentaram crânios significativamente maiores que as fêmeas. Rios de grande porte parecem ter participado na diferenciação genética e estruturação filogeográfica das espécies. O padrão filogeográfico encontrado sugere ao menos dois centros de diversificação para o grupo, um no escudo das Guianas, envolvendo as espécies ao norte do rio Amazonas, e outro no escudo brasileiro, envolvendo *M. glirina* e *M. domestica*.

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ABSTRACT

Short-tailed opossums of the *Monodelphis brevicaudata* complex inhabit northern South America, and comprise three described species - *M. brevicaudata, M. glirina*, and *M. palliolata* - and two undescribed forms already recognized in prior studies. Species delimitation based solely on morphological features is difficult, and because of that many nominal taxa have been associated with this species complex, and several taxonomic arrangements have been proposed. Previous molecular phylogenetic studies using specimens of this species complex revealed substantial genetic divergence rates. The present study aims to elucidate the systematics of the *M. brevicaudata* species complex through the analyses of molecular and morphological characters. We performed phylogenetic analyses on two mitochondrial genes (cyt b and 16S), studied the external and cranial morphology, and investigated whether observed genetic variation is congruent with morphological differences. Our morphological results were generally concordant with the molecular results. We recognize nine species in the species complex. *M. brevicaudata*, *M. palliolata*, and *M. glirina* are considered valid species; *M. touan* is re-established from the synonymy of *M. brevicaudata* and two new species are described and named; the species *M. domestica* proved to be closely related to specimens of the *M. brevicaudata* complex, and thus are considered as part of that group; we also recognized two new species without formallly naming them; *M. maraxina* is considered a synonym of *M. glirina*. Sexual dimorphism is observed in the species, and in two species males showed skulls significantly larger than females. Major rivers seem to have played an important role in generating genetic differentiation and phylogeographical structure of the species. The phylogeographical pattern suggests at least two diversification centers for the group, one in the Guiana shield, comprising species ranging north of the Amazon river, and another in the Brazilian shield, comprising *M. glirina* and *M. domestica*.

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INTRODUÇÃO

Os marsupiais da família Didelphidae pertencem à ordem Didelphimorphia e formam um grupo monofilético (Jansa & Voss, 2000; Voss & Jansa, 2003) fundamentalmente Neotropical, excetuando-se a espécie *Didelphis virginiana* Kerr, 1792 que alcança a região temperada do território norte-americano (Gardner, 1973). Constitui a família de marsupiais mais diversa da região Neotropical, com 19 gêneros e 95 espécies recentes descritas (Gardner, 2007), sendo que e a sua diversidade ainda está sendo descoberta (e. g., Lew, Pérez-Hernández & Ventura, 2006; Solari, 2004; Solari, 2007; Voss, Lunde & Jansa, 2005; Voss, Lunde & Simmons, 2001; Voss, Tarifa & Yensen, 2004), e muitos grupos necessitam de revisões taxonômicas (Brown, 2004).

Neste contexto inclui-se o gênero *Monodelphis* Burnett, 1830, que engloba marsupiais de porte relativamente pequeno, distintos por seus membros e cauda curtos, popularmente conhecidos como catitas-de-rabo-curto. Possuem hábito terrestre a semi-fossorial, orelhas relativamente pequenas e olhos médios a pequenos (Pine & Handley, 2007) e são predadores (Anderson, 1997; Emmons & Feer, 1997). Os espécimes do gênero *Monodelphis* aparentemente estão entre os didelfídeos menos adaptados à vida arbórea (Nowak, 1999).

Monodelphis ccorre desde o Panamá até a Argentina, incluindo florestas úmidas, cerrados, campos e regiões semi-áridas como o Chaco e a Caatinga no Nordeste do Brasil (Costa & Patton, 2006), sendo encontrados desde o nível do mar até cerca de 3.500 metros de altitude (Solari, 2007).

O gênero *Monodelphis* é o mais diverso da família Didelphidae. Segundo Pine & Handley, 2007, a diversidade dentro do gênero, indicada por comparações morfológicas e

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análises de DNA, justifica ao menos a divisão em nível subgenérico, mas as afinidades entre as espécies permanecem muito obscuras para permitir que esta divisão seja feita no presente.

Atualmente, 20 espécies estão descritas para o gênero *Monodelphis* (Pine & Handley, 2007). Destas, várias foram descritas ou tiveram seu status taxonômico alterado recentemente (*e. g.* Lemos, Weksler & Bonvicino, 2000; Lew & Pérez-Hernández, 2004; Solari, 2004; Ventura, Pérez-Hernández & López-Fuster, 1998; Voss *et al.*, 2001), o que evidencia o conhecimento ainda incompleto da taxonomia e diversidade do grupo.

A espécie *M. brevicaudata* (Erxleben, 1777) e táxons afins, ou complexo *brevicaudata*, distribui-se ao norte da América do Sul, no bioma amazônico. De forma geral, os representantes do complexo *brevicaudata* possuem tamanho relativo médio a grande para o gênero e diferenciam-se das espécies congenéricas distribuídas da Amazônia por possuírem a pelagem lateral amarelada a avermelhada, sendo a pelagem cinza limitada a uma faixa longitudinal no dorso (figura 1). O ventre possui coloração levemente ou muito diferenciada das laterais, podendo apresentar-se nos tons creme acinzentado a alaranjado.

Segundo Eisenberg, 1989, *Monodelphis brevicaudata* (*sensu lato*) ocorre mais frequentemente em florestas úmidas do que em florestas decíduas secas, mas podem ser encontrada em habitats de borda em torno de clareiras.

Os animais do grupo possuem hábito solitário (Emmons & Feer, 1997; Linares, 1998). Husson, 1978 e Emmons & Feer, 1997 consideraram *Monodelphis brevicaudata* (*sensu lato*) como noturna, enquanto Eisenberg, 1989 a considerou predominantemente crepuscular. Entretanto, Linares, 1998 e Engstrom, Lim & Reid, 1999 consideraram a espécie e ou espécies

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do grupo *brevicaudata* como diurnas.

FIGURA 1. Exemplar de *Monodelphis brevicaudata* (SLF 325), do sexo masculino, procedente de Porto Trombetas, Oriximiná, Pará, Brasil.

Linares, 1998 reconhece as espécies do grupo como possuindo um número populacional aparentemente baixo, com a dieta composta majoritariamente de insetos e outros invertebrados. Segundo Linares, 1998, os exemplares do gênero costumam passar por entre troncos, ramos caídos e pedras, procurando ativamente insetos, artrópodes, ovos e pequenos animais.

Como reconhecido atualmente, o complexo brevicaudata compreende três espécies- *M. brevicaudata* (Erxleben, 1777)*, M. glirina* (Wagner, 1842) e *M. palliolata* (Osgood, 1914) – e duas formas não descritas, denominadas espécies "A" e "D" por Pine & Handley, 2007. O grupo *Monodelphis brevicaudata* é um exemplo da complexidade taxonômica no gênero. Desde a descrição de *Didelphis brevicaudatus* Erxleben, 1777, 14 táxons nominais já foram associados a este complexo (compilado de Pine & Handley, 2007), e diversos arranjos

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taxonômicos foram propostos, tendo sido reconhecidas de uma (Thomas, 1888) a cinco espécies (Pine & Handley, 2007). A variação geográfica na coloração da pelagem, para a qual o significado taxonômico é difícil de ser avaliado (Voss *et al.*, 2001), e a amostragem geograficamente restrita utilizada pelos autores, aparentemente tem contribuído em maior parte para a complexidade taxonômica no grupo.

Revisões taxonômicas do complexo brevicaudata foram publicadas por Ventura *et al.*, 1998 – para as espécies venezuelanas – e por Voss *et al.*, 2001 – para as espécies amazônicas, com ênfase nas espécies da região das Guianas. Ventura *et al.*, 1998 reconheceram duas espécies do complexo *brevicaudata* na Venezuela: *M. brevicaudata*, considerada como uma forma politípica representada por *M. b. brevicaudata* ao sul do rio Orinoco e *M. b. palliolata* ao norte desse rio; e *M. orinoci* (Thomas, 1899), a qual os autores revalidaram e associaram aos espécimes provenientes dos Llanos Venezuelanos. Os autores justificaram o reconhecimento de *M. orinoci* como uma espécie válida demonstrando haver diferenças significativas do crânio desta em relação à espécie *M. brevicaudata*, além das diferenças externas de pelagem reconhecidas anteriormente (Pérez-Hernández, 1988) e de indicativos de diferenças ecológicas relacionadas ao habitat.

Voss *et al.*, 2001 consideraram *M. brevicaudata* como monotípica, revalidaram *M. glirina* e *M. palliolata*, descrevendo características externas que as distinguem, e reconheceram uma forma não descrita (denominada *Monodelphis* "espécie D" por Pine & Handley, 2007). De acordo com Voss *et al.*, 2001, *M. brevicaudata* está distribuída na sub-região amazônica das Guianas, que inclui a Venezuela ao sul do rio Orinoco, Guiana, Suriname, Guiana Francesa e Brasil a leste do rio Negro e ao norte do rio Amazonas *M. glirina* ocorre na Bolívia e Brasil ao sul do rio Amazonas e a oeste do rio Xingu; *M. palliolata* ocorre a oeste do rio Orinoco no norte da Venezuela e nordeste da Colômbia; e a forma não descrita ocorre ao sul do rio Amazonas e a oeste do rio Xingu (figura 2). Embora Voss *et al.*, 2001 não tenham

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analisado espécimes dos Llanos Venezuelanos associados a *M. orinoci* por Ventura *et al.*, 1998, eles examinaram o tipo de *Peramys brevicaudatus orinoci* Thomas, 1899 e o consideraram como um sinônimo de *M. brevicaudata*. Considerando estas conclusões, Pine & Handley, 2007 reconheceram os espécimes dos Llanos Venezuelanos e Cordilheira Central da Venezuela (associados a *M. orinoci* por Ventura *et al.*, 1998) como uma forma ainda sem nome disponível, denominada *Monodelphis* "espécie A".
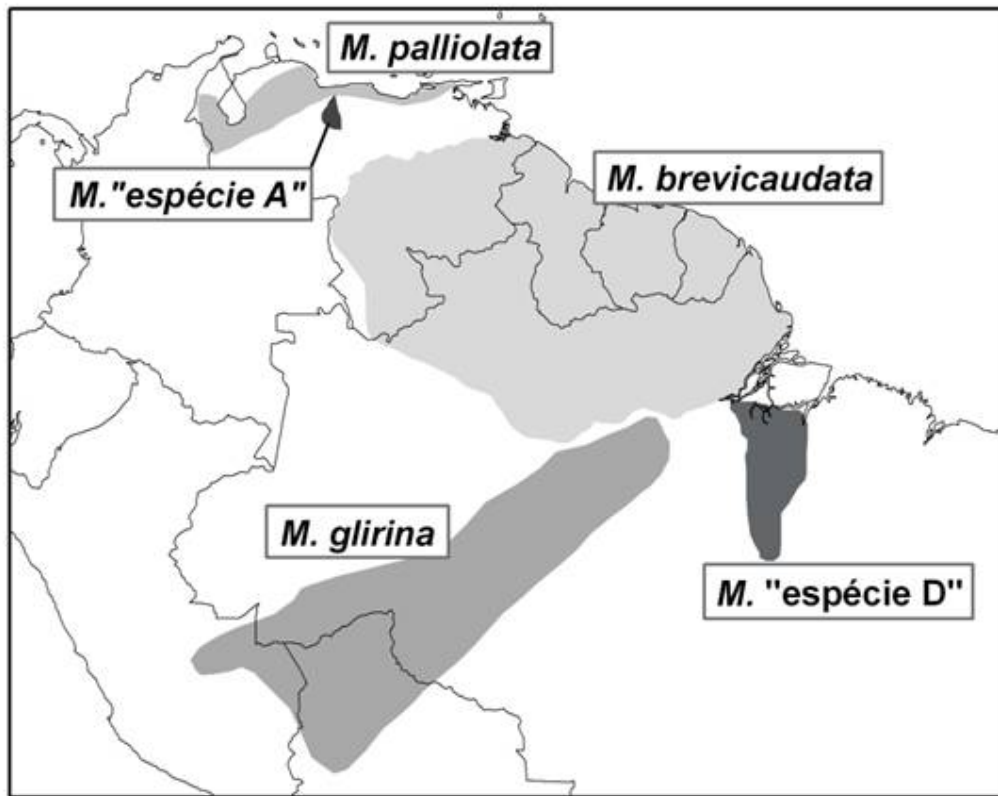
FIGURA 2. Distribuição geográfica das formas atualmente reconhecidas para o complexo *Monodelphis brevicaudata*. Modificada de Pine & Handley, 2007.

As informações disponíveis sobre as relações filogenéticas da espécie e do complexo brevicaudata são poucas e inconclusivas. Apenas três trabalhos investigaram as relações filogenéticas entre espécimes do grupo, todos baseados em dados moleculares do gene

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mitocondrial citocromo b (e. g. Costa & Patton, 2006; Patton & Costa, 2003; Steiner & Catzeflis, 2004). Apesar das relações filogenéticas no grupo não estarem esclarecidas, fica evidente que este complexo apresenta altas taxas internas de divergência genética.

Patton & Costa, 2003 e Costa & Patton, 2006 utilizaram duas amostras do grupo brevicaudata, uma de Manaus, estado do Amazonas (Amazônia central), e outra de Marabá, estado do Pará (sudeste da Amazônia). Esses espécimes exibiram grande divergência genética (pouco superior a 12% nos dois trabalhos) e formaram um clado politômico bem apoiado (pouco superior a 90% de bootstrap nos dois trabalhos) que inclui um espécime de *M. domestica*, uma espécie conhecida principalmente para ambientes de Cerrado e Caatinga.

Steiner & Catzeflis, 2004 analisaram os padrões de variação genética e estruturação geográfica de cinco espécies de marsupiais distribuídas na região das Guianas: *Marmosops parvidens*, *Marmosops pinheiroi*, *Marmosa murina*, *Micoureus demerarae* e *Monodelphis brevicaudata*. Destas, *M. brevicaudata* foi a única espécie que apresentou altos valores de divergência genética dentro da Região das Guianas (7.4% de divergência entre espécimes do norte e centro-sul da Guyana) (figura 3). Os autores observaram que as amostras de *M. brevicaudata* formam um grupo monofilético (98% de bootstrap), com uma divergência genética superior a 13% de *M. glirina*, seu grupo irmão. Dentro de *M. brevicaudata*, o clado bem apoiado (100% de bootstrap) composto por amostras da Venezuela e norte da Guiana divergiu geneticamente em 6.9% do clado não sustentado (<50% de bootstrap) composto pelas amostras do Brasil e da Guiana Francesa. Neste último grupo, a amostra de Manaus divergiu 6.5% em relação ao clado formado pelas amostras do Pará e Guiana Francesa, que agrupou com suporte relativamente alto (89 de bootstrap). A despeito da considerável distância geográfica entre os espécimes amostrados, (de Marábá, Pará, Brasil, e da Guiana Francesa), este clado apresentou uma divergência genética relativamente baixa (2.5%).
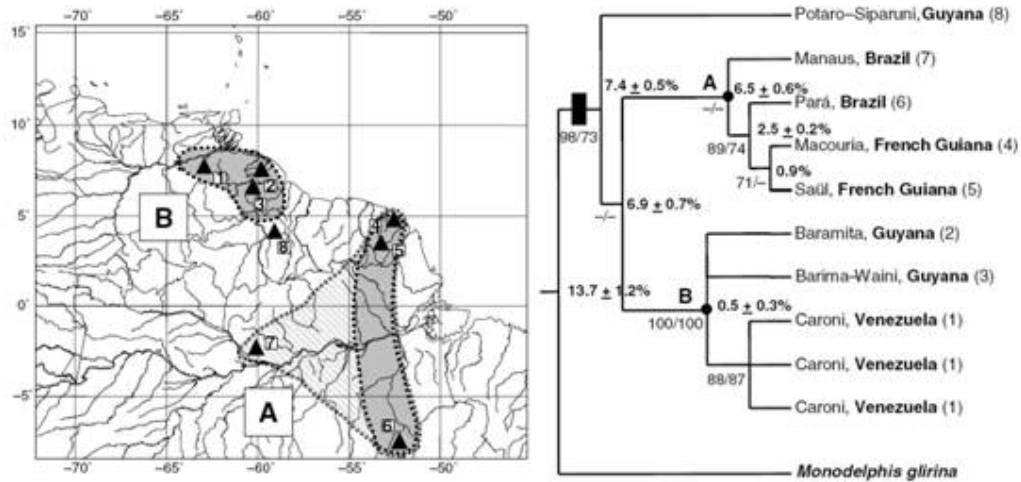
FIGURA 3. Mapa das localidades amostradas na Região das Guianas por Steiner & Catzeflis, 2004 para *Monodelphis brevicaudata*. Áreas em coloração cinza representam os dois clados (A e B) observados na árvore de máxima parcimônia. Como o haplótipo de Manaus (7) não obteve apoio por valores de bootstrap, teve sua ligação ao clado A representada pela linha pontilhada. O retângulo de cor preta na árvore indica monofilia das seqüências de *M. brevicaudata*. Distância genética e valores de bootstrap (acima de 50%) estão indicados ao longo dos ramos para os métodos de máxima parcimônia e máxima verossimilhança (valores de bootstrap inferiores a 50% estão representados por "-"). As sequências de *M. brevicaudata* de Manaus (7) e Pará (6) são as mesmas utilizadas por Patton & Costa, 2003.

O presente trabalho buscou elucidar a sistemática do complexo de espécies *M. brevicaudata* através do estudo dos padrões de variação morfológica e genética. Para tal, desenvolvi análises filogenéticas baseadas em dois genes mitocondriais: citocromo b e 16 S rDNA. Adicionalmente, estudei a morfologia externa e craniana dos espécimes, investigando se existe congruência entre a variação genética e morfológica. Segui o Conceito Filético Geral de Espécie (CFGE) (= General Lineage Species Concept - GLSC - de Queiroz, 1998; de Queiroz, 2005; de Queiroz, 2007) como um conceito primário para delimitação de espécies, e utilizei caracteres morfológicos para caracterizá-las. Segundo o CFGE, uma espécie corresponde a uma linhagem metapopulacional evoluindo separadamente, que é também monofilética em termos de seus componentes genéticos, organismos ou subpopulações. Portanto, deve ser diagnosticável e evolutivamente independente de outras populações (Aleixo, 2007).

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São fornecidas diagnoses, descrições (somente nos casos de espécies novas), comparações morfológicas, distribuição e notas sobre variação geográfica, sexual e etária para os taxa reconhecidos do presente estudo.

Os métodos e os resultados encontrados durante o estudo são apresentados a seguir, em formato de artigo, em língua inglesa. A formatação segue a da revista *Zoological Journal of the Linnean Society*.

Ao todo, foram incluídos 86 espécimes de *Monodelphis* do complexo *brevicaudata* nas análises moleculares e 674 espécimes do grupo foram examinados morfologicamente.

As analises morfológicas foram, em geral, congruentes com as moleculares. São formalmente reconhecidas nove espécies para o complexo brevicaudata, sendo uma revalidada e duas novas, as quais foram descritas e nomeadas. Algumas das formas reconhecidas representam, possivelmente, um complexo de espécies. Adicionalmente, uma espécie foi sinonimizada e duas espécies reconhecidas como distintas permanecem sem uma descrição formal. Rios de grande porte parecem ter participado na diferenciação genética e estruturação filogeográfica das espécies. O padrão filogeográfico encontrado sugere ao menos dois centros de diversificação para o grupo, um no escudo das Guianas, envolvendo as espécies ao norte do rio Amazonas, e outro no escudo brasileiro.

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Species diversity in the *Monodelphis brevicaudata* complex inferred from molecular and morphological data.

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ABSTRACT

Short-tailed opossums of the *Monodelphis brevicaudata* complex inhabit northern South America and comprise three described species - *M. brevicaudata, M. glirina*, and *M. palliolata* - and two undescribed forms already recognized in prior studies. Species delimitation based solely on morphological features is complicated, therefore many nominal taxa have been associated with this complex, and several taxonomic arrangements have been proposed. The few molecular phylogenetic studies using specimens of this complex revealed substantial pairwise genetic distances. We studied the systematics of the *M. brevicaudata* species complex through a combination of molecular and morphological characters. We performed phylogenetic analyses based on two mitochondrial genes (cyt b and 16S), studied the external and cranial morphology, and investigated whether observed genetic variation is congruent with morphological differences. Our morphological analyses were generally concordant with the molecular ones. We recognize nine species in this complex. *M. brevicaudata, M. palliolata*, and *M. glirina* are valid species, although the former is restricted to northern Guyana, Venezuela south of the Orinoco river and northwest of Brazil. *M. touan* is re-estabilished from the synonymy of *M. brevicaudata*, and two new species are described and named. *M. domestica* proved to be closely related to the *M. brevicaudata* complex, and is therefore considered part of that group. We also recognize two new species, which we treat without formal descriptions. *M. maraxina* is considered a synonym of *M. glirina*. *M. glirina and Monodelphis* sp. from Trombetas exhibited significant sexual dimorphism in many cranial dimensions. Rivers seem to have played an important role in generating the genetic differentiation and phylogeographic structure within this complex. The phylogeographic patterns recovered suggest at least two main diversification centers , one on the Guiana shield, comprising species distributed north of the Amazon river, and other on the Brazilian shield, comprising *M. glirina* and *M. domestica*.

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INTRODUCTION

Although in recent years there has been considerable increase in alternative methods for delimiting species, the majority of recognized species worldwide presumably have been delimited and described based solely on morphological differences (Wiens, 2007). However, species delimitation using morphology is complicated in both cryptic and polytypic species (e.g. Chippindale *et al.*, 2004; Mueller *et al.*, 2004). Recently, molecular phylogenies combined with traditional morphological data have shown to be useful in delimiting species with accuracy, potentially overcoming taxonomical problems in many groups with complex morphological polymorphisms and confusing taxonomic histories (e. g. Angulo & Reichle, 2008; Mulcahy, 2008; Stephen, Eriksen & Katz, 2008; Torrez-Pérez *et al.*, 2009).

Short-tailed opossums of the *Monodelphis brevicaudata* complex are a widespread group that inhabits the Amazonian rainforests in northern South America. Specimens of this complex are distinguished from other Amazonian congeneric species by their body pelage pattern, which is comprised of yellowish to reddish lateral fur limiting the longitudinal gray fur to the middorsum. As currently recognized, this complex comprises three species - *M. brevicaudata* (Erxleben, 1777)*, M. glirina* (Wagner, 1842), and *M. palliolata* (Osgood, 1914) - and two undescribed forms, called species "A" and "D" by Pine & Handley, 2007.

The taxonomy of *M. brevicaudata* has always been problematic. Since Erxleben, 1777 described *Didelphis brevicaudatus*, 14 nominal taxa have been associated with this complex (compiled from Pine & Handley, 2007), and several taxonomic arrangements have been proposed, with one (Thomas, 1888) to five species recognized (Pine & Handley, 2007). The conspicuous geographic variation in pelage color within this group, for which the taxonomic significance is difficult to evaluate (Voss *et al.*, 2001), and the geographically restricted samples used by authors appear to be the main contributors to its confusing taxonomy.

Partial taxonomic reviews have been published for the *M. brevicaudata* complex (Ventura *et al.*, 1998 for Venezuelan species; Voss *et al.*, 2001 for Amazonian species with emphasis on taxa from the Guiana region). Ventura *et al.*, 1998 recognized two species of the *M. brevicaudata* complex as occurring in Venezuela: *M. brevicaudata*, which was considered a polytypic species represented by *M. b. brevicaudata* to the south of Rio Orinoco and *M. b. palliolata* to north; and *M. orinoci* (Thomas, 1899), which the authors resurrected from *M. brevicaudata*, and associated to specimens from the Venezuelan Llanos. The authors justified the recognition of *M. orinoci* as full species by demonstrating that there are significant skull

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differences, when compared to the other Venezuelan *Monodelphis* species, in addition to previously recognized external differences (Pérez-Hernández, 1988), and the suggestion of ecological differences among them, associated to habitat differences. Voss *et al.* (2001) considered *M. brevicaudata* as monotypic, re-established *M. glirina* and *M. palliolata* from *M. brevicaudata*, and recognized an unnamed form (later called *Monodelphis* "species D" by Pine & Handley, 2007), describing external differences among *M. brevicaudata* and the three remaining recognized species. According to these authors, *M. brevicaudata* is restricted to the Guiana subregion of Amazonia, including Venezuela south of Rio Orinoco, Guianas, and Brazil east of Rio Negro and north of Rio Amazonas; *M. glirina* occurs in Bolivia and Brazil south of Rio Amazonas and west of Rio Xingu; *M. palliolata* occurs west of Rio Orinoco in northern Venezuela and northeastern Colombia; and the unnamed form occurs south of Rio Amazonas and east of Rio Xingu. Voss *et al.* (2001) did not analyze specimens from the Venezuelan Llanos associated to *M. orinoci* by Ventura *et al.*, 1998, but they examined the holotype of *Peramys brevicaudatus orinoci* Thomas, 1899 and considered it to be *M. brevicaudata*. Considering these conclusions, Gardner (2005) and Pine & Handley (2007) associated the specimens from the Llanos and Cordillera Central in Venezuela (regarded as *M. orinoci* by Ventura *et al.*, 1998 and other authors) to an unnamed form, referred to as *Monodelphis* species A by Pine & Handley, 2007 (Figure 1).

Only a few phylogenetic studies have sampled specimens of this complex (Costa & Patton, 2006; Patton & Costa, 2003; Steiner & Catzeflis, 2004), and only one includes more than two specimens (Steiner & Catzeflis, 2004). These three studies employed sequences of the mitochondrial cytochrome b (cytb) gene, and revealed substantial genetic divergence among specimens currently assigned to *Monodelphis brevicaudata* (sensu Voss *et al.*, 2001). Patton & Costa, 2003 and Costa & Patton, 2006 included two samples of the *M. brevicaudata* complex, one from Manaus, Amazonas (central Amazonia), and one from Marabá, Pará (southeastern Amazonia). The specimens exhibited high pairwise genetic divergences (slightly over 12% in both studies) and formed a well supported clade (92 and 93% bootstrap) with one specimen of *M. domestica*, which inhabits open biomes in South America. Steiner & Catzeflis, 2004 included specimens from French Guiana, Guyana, Venezuela, the two specimens previously used by Patton & Costa, 2003 and Costa & Patton, 2006, and one specimen of *M. glirina* (sensu Voss *et al.*, 2001). The authors found that specimens of *M. brevicaudata* and the specimen from Marabá (*Monodelphis* "species D", sensu Pine & Handley, 2007) formed a monophyletic group (98/73% bootstrap). *M. glirina* was placed as the sister to *M. brevicaudata* clade (genetically divergent by more than 13%), confirming the strong genetic separation between *M.*

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brevicaudata and *M. glirina*. Within *M. brevicaudata* clade, two divergent clades could be distinguished, with the specimen from Potaro-Siparuni, central Guyana, appearing in a basal position in relation to these two clades, showing a genetic divergence of 7.4% relative to them. Specimens from Venezuela and north Guyana formed one of these clades (100% bootstrap), that diverged 6.9% in relation to specimens from Brazil (Manaus and Marabá) and French Guiana. Within this second clade, the specimen from Manaus is basal, diverging 6.5% in relation to specimens from French Guiana and Marabá. Finally, individuals from French Guiana are closely related to Marabá haplotype (89/74% bootstrap), despite the impressive geographical distance separating these localities when compared to those separating French Guiana from either Guyana and Venezuela. Haplotypes from French Guiana diverged from the Marabá sequence by only 2.5% genetic distance.

The present study aims to elucidate the systematics of the *M. brevicaudata* species complex through a combination of molecular and morphological characters. For that, we performed phylogenetic analyses on two mitochondrial genes: cytochrome b and 16S rDNA. Additionally, we studied the external and cranial morphology of the specimens, and investigated whether the observed genetic variation were congruent with morphological differences. We followed the General Lineage Species Concept (GLSC) (de Queiroz, 1998; de Queiroz, 2005; de Queiroz, 2007) as a primary concept to delimit species, and afterwards used morphology to characterize them. Under the GLSC, a species is a separately evolving metapopulation lineage that is also monophyletic in terms of its component genes, organisms, or subpopulations. Therefore, it must be both diagnosable and evolutionarily independent compared to other populations (Aleixo, 2007). We provide diagnoses, descriptions (only in new species cases), morphological comparisons, geographic distributions, and notes on geographic and non-geographic variation for the taxa herein recognized.

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MATERIAL AND METHODS

Phylogenetic analyses

Partial sequences of cytb (471 base pairs) and 16S rDNA (412 bp) were obtained for 64 specimens assigned to the *Monodelphis brevicaudata* complex, including samples from *M. glirina* (18 specimens for 16S and 14 for cytb)*, M. brevicaudata* (30 for 16S and 24 for cytb) and *Monodelphis* "species D" of Pine & Handley, 2007 (15 specimens for 16S and 12 for cytb) (Appendix A). *M. palliolata* and specimens assigned to *Monodelphis* "species A" of Pine & Handley, 2007 were not accessed through molecular data. In addition, we obtained partial sequences of *M. domestica* (14 specimens for 16S and 11 for cytb), a species that clustered with specimens of *M. brevicaudata* in previous phylogenetic studies (see Patton & Costa, 2003, and Costa & Patton, 2006). Because the phylogenetic affinities of the *M. brevicaudata* complex to other congeneric species is unknown, we used samples of the following additional species: *M. emiliae*, *M. iheringi*, *M. kunsi*, *M. scalops*, and *M. sorex* (Appendix A). Our tissue samples were either collected by the Mammalogy and Herpetology staff at the Museu Paraense Emílio Goeldi (MPEG), or obtained through loans and donations (see Acknowledgments). In addition to the sequences obtained from the tissue samples mentioned above, we used four partial sequences of cytb through the courtesy of Dr. James L. Patton (Musem of Vertebrate Zoology, University of California at Berkley) and 12 sequences (10 of cytb and two of 16S rDNA) from GenBank, including *Didelphis marsupialis* and *Caluromys philander*, which were considered as outgroups for rooting trees in all phylogenetic analyses (Appendix A).

DNA was extracted from ethanol-preserved tissues using phenol-chloroform, proteinase K-RNAse methods (Sambrook, Fritsch & Maniatis, 1989). Sequences were amplified by the polymerase chain reaction (PCR) using conserved primers: L1987 (5'-GCCTCGCCTGTTTACCAAA-3') and H2609 (5'-CCGGTCTGAACTCAGATC-3') for 16S (Palumbi *et al.*, 1991); and IECOS F1 (5'-TGGCATGAAAAACCATYGTT-3') and IECOS R1 (5'-CCTTCRTTGTTGGCTTACAA-3') for cyt-*b* (Wilsea Figueiredo*,* pers. comm.). The conditions for cytb consisted of an initial denaturation at 94° C (3min), followed by 35 cycles comprising denaturation at 94° C (30 s), annealing at 55° C – *M. kunsi* ; 58° C – *M. brevicaudata* and *M.* "species D"; 60° C – *M. glirina* and *M. domestica*; and 63° C – *M. emiliae*, *M. iheringi*, *M. scalops* and *M. sorex* (1 min), and extension at 72° C (2 min), with a final extension at 72° C (7min). 16S rDNA amplification conditions consisted of an initial denaturation at 94° C (3min), followed by 30 cycles comprising denaturation at 94° C (30 s), annealing at 50° C (1 min) and extension at 72° C (2 min), with a final extension at 72° C

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(7min). Only the forward strands of 16S rDNA and cytb fragments were sequenced, both using an automatic sequencer ABI 377 (Applied Biosystems Inc.- Perkin–Elmer).

Cytb and 16S rDNA sequence alignments were performed manually using BioEdit 7.0.8.0 (Hall, 1999) and complemented with Clustal W of MEGA 4 (Tamura *et al.*, 2007). Phylogenetic relationships were inferred with Bayesian analyses implemented in Mr. Bayes 3.1 (Ronquist, Huelsenbeck & van der Mark, 2005), by maximum-likelihood analyses (ML) implemented in Garli 0.951 (Zwickl, 2006), by parsimony analyses (MP) implemented in PAUP* 4.0 b10 (Swofford, 2002), and by neighbor joining analyses (NJ) implemented in MEGA 4. We also calculated p corrected distances for all pairwise comparisons in MEGA 4.

Modeltest 3.1 (Posada & Crandall, 1998) was employed to select the model of nucleotide substitution that best fits our data. The Hasegawa Kishino Yano (HKY) model, with allowance for gamma distribution of rate variation (G=1.4187) and for a proportion of invariant sites (I=0.6092), best fit the cytb data set using the Bayesian information criterion. The General Time Reversible model (GTR), with allowance for gamma distribution of rate variation (G=0.1649), best fit the 16S rDNA data set using the Bayesian information criterion. The HKY model, with allowance for gamma distribution of rate variation (G=1.2482) and for a proportion of invariant sites (I=0.6359), best fit the combined matrices data set using the Bayesian information criterion.

Bayesian analyses were performed using two independent runs of four Markov chains (1 cold and 3 heated) with 3×10^6 generations and sampling every 100 generations. The first 25% of the sampling trees and estimated parameters were burned off to allow the chains to reach stationarity. ML analyses were performed using the models and parameters obtained by Modeltest, in a heuristic search, using the tree bisection and reconnection algorithm (TBR) and random addition of taxa. NJ analyses were performed using Tamura Nei evolutionary model, and gamma distribution shape parameter established by Modeltest (TN+G). These options were used to calculate distances for all pairwise comparisons. MP analyses were performed using heuristic searches and random addition of taxa and the TBR. A total of 10,000 replications was determined for the search, and the number of most parsimonious trees stored in the memory was limited to five for each replicate. Reliability of clades was evaluated by Bayesian posterior probabilities , or by bootstrap analyses (Felsenstein, 1985) with 100 replications for MP analyses and 1000 replications for NJ analyses.

Specimens and localities

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We examined 674 specimens of the *M. brevicaudata* complex, preserved as skulls, skins and fluid material in the following collections: MPEG - Museu Paraense Emílio Goeldi, Belém; IEPA - Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá; MNRJ - Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo; LZUFPI - Laboratório de Zoologia Prof. Antônio J. Dumbra, Universidade Federal do Piauí, Teresina; USNM - National Museum of Natural History, Washington, D.C.; AMNH - American Museum of Natural History, New York; FMNH - Field Museum of Natural History, Chicago; ISEM V- Institut des Sciences de l'Evolution, Montpellier. In addition, we examined uncataloged specimens cited by field numbers. Specimens examined are listed in Appendix B.

Holotypes, some vouchers and important complementary specimens were analyzed through photographs (also cited in the Appendix B) provided by the curators of several mammal collections, as follows: Natural History Museum, London (holotypes of *Didelphis brevicaudata* [skull: BMNH 67.4.12.540], *Peramys brevicaudatus orinoci* [skin/skull: BMNH 98.12.1.22], *Didelphis hunteri* [skull: BMNH 88.1.31.1], *Monodelphis maraxina* [skin/skull: BMNH 23.8.9.9], and *Didelphis domestica* [skin/skull: BMNH 87.10.25.1]); Field Museum, Chicago (holotype of *Peramys palliolatus* [skin/skull: FMNH 20524]); Royal Ontario Museum, Toronto (specimens of the *M. brevicaudata* complex from Barima-Waini, Guyana, GenBank accession number AJ606461 [skin/skull: ROM 98909]; and from Potaro-Siparuni, Guyana, GenBank accession number AJ606462 [skin/skull: ROM 108477]); Instituto Nacional de Pesquisas da Amazônia, Manaus (specimen of the *M. brevicaudata* complex from Conjunto Parque do Rouxinol, Manaus [preserved in fluid: INPA 2854]. The holotype of *Peramys dorsalis* (skull: AMNH 16126) was analyzed through pictures available on the AMNH website. The neotype of *Viverra touan* (skin/skull: FMNH 21720) was analyzed through pictures published in Voss *et al*. (2001). Four specimens of the *M. brevicaudata* complex from Rio Jufari, states of Amazonas and Roraima, Brazil (skin: CGB 80, 81, 82, 90) were analyzed through pictures provided by C. G. Bantel, and three specimens of the *M. brevicaudata* complex from Rio Caroni, Bolívar, Venezuela (skin: L-1917, 1918, 1920, GenBank access number AJ606460, AJ606459, AJ606458) were analyzed through pictures provided by O. Linares.

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Age Criteria

The age classification employed in this report is a refinement of that proposed by Tribe, 1990, which was based on the pattern of tooth eruption he observed in didelphids (including *Marmosa* and *Didelphis*). In *Marmosa*, the deciduous third premolar, dP3, is not replaced until M4 has erupted; therefore, P3 is the last upper tooth to erupt. In *Didelphis*, the M4 does not erupt until dP3 is replaced by P3; therefore, M4 is the last upper tooth to erupt. Similarly to *Didelphis*, M4 is the last upper tooth to erupt in specimens of the *Monodelphis brevicaudata* complex; however, by the time M4 erupts, P3 is not fully grown (or nearly so) as occurs in *Didelphis*. Therefore, M4 eruption occurs immediately after P3 eruption, and the development of both teeth occurs simultaneously. As a result, while specimens of *Didelphis* belonging to Tribe's age class 4 have P3 erupting, M4 unerupted, and M3 fully grown or nearly so, specimens of the *M. brevicaudata* complex belonging to age class 4 (defined by us) have both P3 and M4 erupting, and M3 fully grown.

Because Tribe's age class 4 is not applicable to the *M. brevicaudata* complex, and older specimens exhibit considerable ontogenetic variation not appropriately assignable to Tribe's age classes 5 to 7, we found it useful to redefine those age classes which are described below.

Age class 4: M1–M3 present, P3 erupting (with dPm3 sometimes still fixed to the maxillae), M4 erupting (generally at the initial or medium growth stage);

Age class 5: M1-M4 present, labial cingulum of P3 emergent but slightly dorsal to labial cingulum of P2 (indicating the penultimate stage of P3 eruption), M3 and M4 cristae unworn or with very narrow and discontinuous strips of exposed dentine;

Age class 6 - Labial cingulum of P3 aligned with or ventral to the labial cingulum of P2 (indicating the complete eruption of P3), dentine narrowly exposed on all M3 cristae and very narrowly exposed on all M4 cristae;

Age class 7 - Dentine broadly exposed along the preparacrista of M3 and narrowly exposed on the other cristae of M3 and M4;

Age class 8 - Dentine broadly exposed on most M3 cristae and narrowly to broadly exposed on the M4 cristae.

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The specimens placed in age classes 1-3 are juveniles (dP3 is still in place), and those in age class 4 are subadults (P3 incompletely erupted). Among adults, we considered specimens placed in age class 5 as early adults (incipient wear in M3), those in age class 6 as intermediate adults (little wear in M3), and those in age classes 7 and 8 as old adults (conspicuous to total wear in M3).

Comparative Morphology

The direct examination of specimens included the search for diagnostic characters on skins and skulls that could be useful to distinguish the clades obtained in the molecular analysis. We priorized comparisons among specimens of the same sex and age classes to avoid characters associated with sexual and age variation, respectively. Nomenclature for cranial osteology follows Wible, 2003, and for external morphology, dental structures, palatine fenestrae and foramina follows Voss & Jansa, 2003.

Measurements

We recorded external measurements (in millimeters) and weight (in grams) from specimen labels. The former include Total length (TL), length of head-and-body (HBL), length of tail (LT), length of hind foot (HF), and length of ear (Ear). When not available on specimen label, length of head-and-body (HBL) was calculated by subtracting LT from TL.

We measured the following 31 craniodental dimensions to the nearest 0.01 mm with digital calipers while specimens were viewed under a stereo microscope.

1. Greatest Length of Skull (GLS): From the anteriormost point of the premaxilla to the posteriormost point of the braincase.
2. Condylo-Basal Length (CBL): From the occipital condyles to the anteriormost point of the premaxillae
3. Rostral Length (RL): From the anteriormost point of the nasals to the anteriormost point of the orbital cavity.
4. Nasal Length (NL): The greatest length of the nasal bone.
5. Palatal Length (PL): Measured in the midline from the anteriormost point of the premaxillae to the end of the palate.
6. Length of Maxillary Toothrow (MTR): From the anterior surface of the base of the upper canine to the posterior margin of M4 crown.

7. Length of Upper Molar Series (UMS): Crown length of the upper molars, from the anterolabial margin of M1 to the posterior margin of M4.

8. Length of Upper Incisors (LUI): From the anterior surface of the base of the second upper incisor to the posterior surface of the base of the fifth upper incisor.

9. Length of M3 (LM3): Length (longitudinal dimension) of the third upper molar crown across paracone and metacone.

10. Width of M3 (WM3): Greatest width (transverse dimension) of the third upper molar, from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

11. Width of M4 (WM4): Greatest width (transverse dimension) of the fourth upper molar, from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

12. Height of Upper Canine (HC): Height (vertical dimension) of C, from the exposed labial base to the tip of the tooth.

13. Palatal Breadth at M3 (PBM3): Measured across the labial margins of the third molar (M3) roots.

14. Post-Palatal Breadth (PPB): Least breadth across the anterior processes of the left and right alisphenoids.

15. Breadth of Basicranium between Foramina Ovale (BFO): Measured across medial margins of foramina ovale on each side.

16. Breadth of Basicranium between Postglenoid Processes (BPG): Measured across medial margins of postglenoid processes on each side.

17. Length of Tympanic Bulla (LTB): Measured from the anterior curvature of the alisphenoid tympanic process to the posteriormost point of the petrosal pars cochlearis.

18. Length of Incisive Foramen (LIF): Greatest anterior-posterior dimension of one incisive foramen.

19. Breadth of Incisive Foramina (BIF): Greatest transverse dimension across one incisive foramen.

20. Length of Maxillopalatine fenestra (LMP): Greatest anterior-posterior dimension of one maxillopalatine fenestra.

21. Breadth of Maxillopalatine fenestra (BMF): Greatest transverse dimension across one incisive foramen.

22. Nasal Breadth (NB): Measured across the triple-point suture of the nasal, frontal, and maxillary bones on each side.

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23. Breadth of Rostrum across Canines (BRC): Measured across the labial base of the upper canine on each side.

24. Breadth of Rostrum across the Orbital Fossae (BRO): Measured across the anteriormost point of the orbital margins on each side.

25. Postorbital Constriction (POC): Measured at the narrowest point across the frontals between the temporal fossae.

26. Breadth of Braincase (BBC): Measured immediately above the zygomatic process of the squamosal on each side.

27. Zygomatic Breath (ZB): Greatest breadth across the zygomatic arches.

28. Length of Mandible (LM): Measured from the anteriormost point of the mandible (medial to the alveolus of i1) to the posteriormost point of the angular process.

29. Height of Mandibular Body (HMB): Height (vertical dimension) of mandibular body measured immediately behind the fourth lower molar (m4).

30. Length of Lower Toothrow (LTR): From the anterior surface of the base of the lower canine to the posterior margin of m4.

31. Length of Lower Molar Series (LMS): Crown length of the lower molars, from the anterolingual margin of m1 to the posterolingual margin of m4.

Measurements on toothrows and mandible were taken on the left side, and those of paired bones or structures were taken on the right side, except when proper measurements were attainable only on the opposite side.

For species with a sufficient sample size, we tested the significance of differences between sexes for each variable using Student's t-test with Bonferroni's correction, and the significance of differences among age classes herein recognized by performing analysis of variance (ANOVA) tests followed by Tukey's multiple comparison tests.

For sexual dimorphism , we performed Student's t-tests with either specimens from a single locality or from one locality plus nearby localities, in order to decrease the influence of geographic variation. Additionally, we only employed specimens from age classes 7 and 8 (old adults, which have similar skull size) to avoid interfere in the results due unequal sample size among classes.

We used size-free discriminant function analysis (dos Reis, Pessôa & Strauss, 1990) to test whether species herein recognized could be differentiated by craniodental measurements. In this analysis we applied the stepwise method, due to the high number of variables and low

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number of individuals in some samples. Therefore, it was selected a lower number of variables (which is not higher than the number of individuals of the smallest sample), consequently increasing the robustness of the analyses.

All statistical analyses were run in SYSTAT 12 for Windows (Systat Software, San Jose, California, USA).

RESULTS

Phylogenetic analyses

All phylogenetic analyses (Bayesian, ML, MP, and NJ) yielded the same groups in the *M. brevicaudata* complex. The *Monodelphis brevicaudata* complex as recognized by Voss *et al.*, 2001 is paraphyletic if *M. domestica* is not included, in all analyses of 16S rDNA, cytb, and combined matrices of molecular data (Figure 2). *M. glirina* (sensu Voss *et al.*, 2001) and *M. domestica* were both recovered as monophyletic lineages. The species *M. brevicaudata* (sensu Voss *et al.*, 2001) is monophyletic in all analyses of 16S rDNA and combined data, and in MP and NJ analysis with cytb data, but not in Bayesian and ML analysis of cytb data.

M. brevicaudata (Voss sensu *et al.*, 2001) is composed of three distinct clades in all analyses, with mean intraspecific pairwise divergences of 4.6% for cytb and 2.6% for 16S rDNA sequences. There is high bootstrap support for the northwestern clade, containing specimens from northern Guyana and Venezuela; the eastern clade, containing specimens from French Guiana, and eastern Brazil (state of Amapá, and eastern Pará); and the central clade, containing specimens from southern Guyana and north of state of Pará, Brazil. Mean pairwise divergence values within these groups (Table 1) are 0.5% (cytb) and 0.36% (16S rDNA) in the northwestern clade; 1.8% (cytb) and 0.59% (16S rDNA) in the eastern clade; and 0.8% (cytb and 16 S rDNA) in the central clade. The addition of a sequence from Manaus, Brazil to cytb and combined data showed in all analyses the existence of a fourth lineage of *M. brevicaudata*. This specimen from Manaus diverges from the northwestern clade by 7.6%, from the eastern clade by 6.9%, and from the central clade by 7.9%. The eastern clade diverges from the northwestern clade by 6.9% (cytb) and 3.2% (16S rDNA), and from the central clade by 6.5% (cytb) and 4.2% (16S rDNA). Central and northwestern clades diverge from each other by 8.2% (cytb) and 3.2% (16S rDNA) (Table 1).

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The relationships among clades of *M. brevicaudata* were the same in all analyses using 16S rDNA and combined data, i.e. the central clade is sister to the northwest clade plus the east clade (Figure 2). The affinities of the central clade changed according to the type of analysis for the cytb data. The central clade was basal to the other *M. brevicaudata* clades in NJ and MP analyses, whereas in Bayesian and ML analyses *M. domestica* was internal to *M. brevicaudata* (Voss sensu *et al.*, 2001), and the central clade is sister to a polytomy incuding *M. glirina*. In all cytb analyses and in ML and MP analysis of combined data including the specimen from Manaus, the latter appears as sister to the northwestern clade. However, this specimen is sister to the eastern clade in NJ analysis using combined data, and in a polytomy including the northwestern and eastern clades in Bayesian analyses according to the combined data (Figure 2). In general, there was no strong support to the relationships among the different *M. brevicaudata* clades, with the exception of the central clade, which is highly supported as sister to the other *M. brevicaudata* clades in most analyses.

Within the eastern clade, haplotypes from the state of Pará, Brazil (south of the Amazon river) comprised a highly supported clade in all analyses. This clade is embedded within haplotypes from French Guiana and the state of Amapá, Brazil (north of the Amazon river), rendering the northern Amazon group paraphyletic with respect to the southern Amazon group (Figure 2). However, both the bootstrap support and posterior probabilities are low in all analyses, and the actual relationship of specimens from north of the Amazon river could not be reached with certainty at this time. Also, the relationships among subgroups of nearby localities from north of the Amazon river did not have high bootstrap or posterior probabilities, resulting in a basal politomy in most consensus trees. Mean pairwise divergence values are 1.2% (cytb) and 0.7% (16S rDNA) within the northern Amazon group, and 0.7% (cytb) and 0.0% (16S rDNA) within the southern Amazon group. These two groups diverge from each other by 2.6% (cytb) and 0.8% (16S rDNA).

Specimens from south of the Amazon river and west of the Xingu river correspond to *Monodelphis glirina*. Additionally, some specimens from east of Xingu river included in the molecular analyses (e.g., those from Canaã dos Carajás and Marabá – see Figure 2) also grouped within *M. glirina*. Despite high mean genetic divergence within this species (4.4% to cytb; Table 1), we found no geographic structur nor well supported clades, such as those observed in *Monodelphis brevicaudata*. The topologies within *M. glirina* were different in each analyses, with subgroups of nearby localities changing their positions to form low supported clades that resulted in a basal politomy in most consensus trees. However, the specimens from

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east Xingu river (Canaã dos Carajás and Marabá) frequently appeared as the sister group to all specimens from the state of Mato Grosso (in all combined data analysis [Figure 2] and NJ analyses of cytb data). Moreover, the specimen from Pando, Bolivia (the westernmost point of our sample, included in cytb and combined analyses), was sister to all other specimens of *M. glirina* in NJ analyses of cytb data (not shown) and in Bayesian analyses of combined data (Figure 2). The Pando specimen diverged from all other conspecific members by 9.8% on average, whereas the remaining specimens showed a mean pairwise divergence of 3.6%. The high divergence value for the Pando specimen suggests the existence of at least two distinct lineages within *M. glirina*, although the basal position of this specimen was neither observed in the remaining analysis, nor supported by high nodal support values.

Other specimens recovered as basal members of all other *M. glirina* specimens include one individual from Jacareacanga for MP analyses of cytb data and specimens from Vitória do Xingu for ML analyses of cytb data. Regarding the cytb sequences, these specimens diverged from all other conspecific members by a mean of 6.4% and 4.0% respectively, while the remaining specimens showed internal mean divergences of 4.1%, and 4.6% respectively. Specimens from east of the Xingu river, an area currently not included in the geographic distribution area of *M. glirina*, exhibited cytb mean divergence of 4.6% from all other conspecific specimens, while the remaining specimens diverged by a mean of 4.4%.

Monodelphis domestica was placed within the *M. brevicaudata* complex, basal to the *M. brevicaudata* clades in most analyses (Figure 2). In the Bayesian and ML analysis of cytb data, however, *M. domestica* grouped more internally than the central clade of *M. brevicaudata*, but with low support values. *M. domestica* showed a internal mean divergence of 3.3% in cytb and 1.25% in 16S rDNA sequences, and comprised two distinct and relatively well supported clades in all analyses: one with specimens from northeast Brazil (called *M. domestica* east – see Figure 2), including states of Piauí, Bahia, and Ceará, with an internal mean divergence of 1.6% in cytb and 0.4% in 16S rDNA sequences; and another with specimens from Goiás, Tocantins, and state of Mato Grosso (called *M. domestica* west – see Figure 2), with an internal mean divergence of 1.6% in cytb and 0.8% in 16S rDNA sequences. These two clades diverge from one another by means of 4.7% in cytb and 1.9% in 16S rDNA sequences.

The relationships of the *M. brevicaudata* complex (including *M. domestica*) with other congeneric species was not clear. NJ and Bayesian analyses with 16S rDNA data (not shown) indicated, with low support values (35% in NJ, 72% in Bayesian analyses), that the *M.*

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brevicaudata complex is more related to *M. emiliae*. In all other analyses, however, *M. emiliae* clusted with other species of *Monodelphis* (Figure 2).

Delimiting species in the *M. brevicaudata* complex

Our morphological analyses were generally concordant with molecular analyses, and showed that the divergent clades we found within *M. brevicaudata* (sensu Voss *et al.*, 2001) correspond to specimens with distinguishable pelage characters, which we recognize in the follow section as distinct species (see Figure 3 for a correspondence between the clade structure found and taxa names associated with them).

Didelphis brevicaudatus Erxleben, 1777 is the oldest available name for specimens of the northwest clade (Figure 3). Its assignment to the clade is supported by the morphological similarity of the specimen ROM 98909 (placed in northwest clade) with the holotype of *M. brevicaudata*, and by the geographic association of the northwestern clade with the type locality of *M. brevicaudata*, restricted to Kartabo, northern Guyana, by Voss *et al.*, 2001.

Viverra touan Shaw, 1800 is the oldest available name for specimens of the east clade, and is here resurrected from the synonymy of *M. brevicaudata* to include specimens of the east clade that come from the localities north of the Amazon river (French Guiana and state of Amapá) (Figure 3). In addition to the genetic differences found, specimens from French Guiana, including the neotype of *Viverra touan* from Cayenne, and from other localities of Amapá are easily distinguished from specimens of *M. brevicaudata* (now restricted) on the basis of morphology. The necessity of including only specimens from north of the Amazon river under the name Monodelphis *touan* (and exclude the southern Amazon group of this name) is explained by the combined results found in molecular and morphological analysis. Specimens within the east clade, but from localities south of the Amazon river (regarded as "species D" by Pine & Handley, 2007) form a proper monophyletic lineage strongly supported in all analyses. Despite the relative low values of genetic divergence between them and the specimens of the east clade from north of the Amazon river (average 2.6%), specimens from south and north are clearly morphologically distinct, and both groups are diagnosable. Therefore, a new name is proposed below for the specimens from south of the Amazon river (Figure 3).

The central clade constitutes a lineage clearly independent from any other found in *M. brevicaudata* complex. As there is no name available for this lineage, we also describe it as a new species below. Morphologically, the voucher specimens of this clade are easily

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distinguished from other specimens of the *M. brevicaudata* complex, except for specimens of *M. touan*, to which they are very similar.

The single voucher specimen of the genetic lineage from Manaus (Figure 4, locality X) is a juvenile specimen preserved in fluid. Although we were not able to determine diagnostic morphologic features for this lineage with such scarce material, the results of the molecular analyses lead us to recognize it as a distinct species, for which we are not aware of any available name. This species, provisionally treated here as *M.* sp. "Manaus", only could be described after the examination of more specimens from this taxon.

Specimens of *M. glirina* included in the molecular analysis showed high intraspecific mean divergence, and the morphological analysis indicated high variability too. However, molecular sub groups formed were variable and, in general, with low support values. Morphologically, we observed important variable features between populations, some of which with a geographical correlation, suggesting that this species may also correspond to a complex of several species. However, with data available at this point, we could not determine with certainty any division.

In this study, we analyzed some specimens from localities on east of the Xingu river labelled as *M. domestica* (from Marabá and São Félix do Xingu). Morphological traits of their skulls revealed more similarities to *M. glirina* than to *M. domestica*. The inclusion of specimens from Marabá in our molecular analysis allowed us to confirm their allocation to *M. glirina* instead of *M. domestica*. However, the general pattern of pelage color actually resemble, at first look, those exhibited by the latter species.

The color pattern observed in specimens of *M. glirina* east of the Xingu river show a striking concordance with description of *M. maraxina* Thomas, 1923, a species described from the Marajó Island, in northeastern state of Pará. The analysis of *M. maraxina* holotype (BMNH 12.5.11.13) confirmed its morphological similarity with the specimens from east Xingu, indicating cospecificity among them, and therefore, *M. maraxina* is treated here as a junior synonym of *M. glirina*.

As mentioned before, specimens assigned to *M. domestica* grouped with specimens of the *M. brevicaudata* complex in our molecular analyses. Moreover, *M. domestica* showed two main clades in all analyses, with geographic structuring and considerable genetic distance, suggesting that two species may be encompassed under this name. The biogeographic interpretation of these results and a taxonomic review of *M. domestica* are beyond the scope

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of this study. However, our analysis of a few specimens of *M. domestica* was essential to provide cranial and pelage characters useful to distinguish this species from *M. glirina* on east of the Xingu river.

Although specimens assigned to *M. palliolata* and *M.* species A of Pine & Handley, 2007 were not included in our molecular samples, our morphological analyses showed that both taxa can be effectively distinguished from each other and from the other species of the *M. brevicaudata* complex herein recognized. Therefore, we recognize both as valid species, but due the scarce material for *M.* "species A" (any skull of adult specimen available) we were not able to describe and name it.

In summary, we recognize nine species in the *Monodelphis brevicaudata* complex, namely *M. brevicaudata*, *M. touan*, *M.* sp. nov "touan sul" (equivalent to *M.* species D from Pine & Handley, 2007), *M.* sp. nov. "Trombetas", *M.* sp. "Manaus", *M. glirina*, *M. domestica*, *M. palliolata*, and *M.* "species A". It is worth noting that *M. glirina* and *M. domestica*)may actually represent species complexes.

Bellow, we provide a general description of the external and craniodental morphology of the species in the *M. brevicaudata* complex, followed by diagnoses of *M. brevicaudata*, *M. palliolata*, *M. glirina*, *M. touan*, and descriptions of the two new species named here. For each of these species, we provide information on type material, geographic distribution, geographic and nongeographic variation, morphological comparisons, and taxonomic remarks. We also provide morphological comments and comparisons about the remaining forms recognized in the group: *M.* sp. "Manaus", *M. domestica*, and *M.* "species A".

Species accounts

The studied species of the *M. brevicaudata* complex share many features, and to avoid repeating attributes in each species diagnose we list below some of the main characteristics observed in skin and skull of those species. The following general diagnosis include *M. brevicaudata*, *M. glirina*, *M. palliolata*, *M. touan*, *M.* sp. nov. "touan sul", and *M.* sp. nov. "Trombetas". The remaining species are not included because they were not sufficiently sampled for thorough morphological analyses; however, certainly most of these characters are also applicable for these forms.

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Species in the *M. brevicaudata* complex share a relative large size for the genus (HBL ≥ 95 and ≤ 183 mm in adult specimens); dorsal fur relatively long (ca. 8 mm); middorsum grayish or brownish; flanks orange or reddish, but some specimens of *M. brevicaudata* and *M. glirina* exhibit no distinction between the middorsal and lateral fur; ventral fur shorter (ca. 4mm) and apparently less dense than dorsal fur; ventral hairs bicolored, gray at the base and cream to orange distally; pelage becomes sparser, shorter, and slightly or considerably more orange/reddish on throat and chin; ears small, uniformly colored, apparently naked; hands and feet with digit III slightly longer than digits II and IV, the latter two subequal in size. Digit V shorter than digits II-IV; halux considerably shorter; plantar surface of foot covered with five enlarged convex tubercles (thenar and four interdigital pads); tail slightly longer than half the head and body`s length.

Skull relatively large for the genus (CBL averages between 31.6 and 45.3 mm in adult specimens); braincase shorter than rostrum; sagital crest and temporal lines weak, commonly present only in adult males; zygomatic arches robust, slightly expanded to laterals and convergent anteriorly (ZB between 53% and 57% of CBL); rostrum broad (BRC between 53% and 57% of the BBC), gently concave in dorsal view at the pre-molars line; premaxillae extend slightly beyond the first upper incisives anteriorly, not forming a distinct rostral process; nasals narrow and parallel anteriorly, somewhat diamond-shaped posteriorly. Interorbital region moderately constricted (POC between 42% and 46% of the BBC); supraorbital crests absent; maxillopalatine fenestra approximately twice the length of incisive foramen. Auditory bulla small (LTB ca. 14-15% of CBL) and incomplete; anteromedial surface of the tympanic process of the alisphenoid pointed or rounded, with no bony strut or lamina connecting with the transverse canal foramen; nuchal crests well defined and developed; post-tympanic processes of the squamosal enlarged; fenestra cochleae of petrosal exposed in ventrolateral view; upper canine robust; second and third premolars (upper and lower) not sharply differentiated in size; upper molars large (UMS ≥ 7.0 and ≤ 9.0 mm); mandibular rami shallow and bowed, but robust, with posterior shelf of masseteric fossa robust.

Monodelphis brevicaudata (Erxleben, 1777)

Type information. Holotype BM 67.4.12.540, an adult female preserved in fluid with an extracted skull. The original type locality *"In Americae australis silvis"* was restricted to Suriname by Matschie, 1916, and reallocated to Kartabo, Guyana, by Voss *et al.*, 2001.

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Synonyms. *brachyuros* Schreber, 1777; *surinamensis* Zimmermann, 1780; *sebae* Gray, 1827; *hunteri* Waterhouse, 1841; *orinoci* Thomas, 1899; and *dorsalis* Allen, 1904.

Morphological Diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 142 mm in adult females and 157 mm in adult males. Dorsal pelage commonly with two colors: a slightly or non grizzled, and brownish or grayish stripe at middorsum, differing from the reddish sides, but with little or no contrast between them (Figure 4). Some specimens show indistinctly middorsal stripe, and some lack it completely, with both middorsal and lateral fur reddish or brownish red; head pelage reddish laterally, with narrow middorsal stripe (when distinguishable), varying from whitish gray or yellowish to orange, confined middorsally by a band of red hairs above each eye; underparts cream-gray, sharply differentiated from the reddish sides (Figure 5); throat and chin distinctly reddish; Mammae at the inguinal/abdominal region, one central and eight distributed circumferentially around it (L-1920); tail covered dorsally by body fur up to about one fourth of the caudal length; ventrally, the body fur is limited to the tail`s connection with the body; CBL averages 35.9 mm in adult females and 39.4 mm in adult males (Table 2); interorbital region relatively narrow (Figure 6); zygomatic arches slightly convergent anteriorly; maxillopalatine foramina proportionally shorter (Figure 7); UMS averages 7.8 mm in adult females, and 7.9 mm in adult males.

Distribution. Restricted to northern Guyana, Venezuela south of Rio Orinoco (in the states of Bolívar and Amazonas), and northwest of Brazil (north of Rio Negro and west of Rio Branco, in the states of Amazonas and Roraima) (Figure 8).

Geographic variation. As mentioned above, the middorsal stripe can be present, absent, or indistinct. As result, the dorsal pelage exhibits 1) distinct bicolored pattern, with middorsal fur brownish or grayish, and laterals reddish (as generally occurs in specimens from Brazil, e.g. MN 69058, 69367, CGB 80, 90, south of Venezuela, e.g. USNM 385010, 388355, 406907, 406910, and east of Venezuela, e.g. AMNH 16125, L-1920, USNM 443781, 448511); 2) indistinctly bicolored pattern, with the middorsal fur darker than laterals, but without a stripe delimited (specimens from east of Venezuela, e.g. USNM 385004, 385005 (Figure 4); and northwestern Guyana, e.g. USNM 568009); and 3) unicolored pattern, with the upperparts homogeneous, from reddish to reddish brown (specimens from north of Guyana, e.g. AMNH 48133, ROM 98909). At the crown, the middorsal stripe is commonly distinct, but quite variable in color and intensity. As an example, specimens from east of the Jufari river, state of Roraima, Brazil, exhibit narrow and yellowish-grizzled stripe, whereas specimens from the opposite margin of

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this river, in the state of Amazonas, exhibit broader and lighter stripe (specimens analyzed through photographs taken by C. Bantel). The size of the specimens is also variable, generally smaller in the northern part of distribution , and larger in southern Venezuela and Brazil.

Remarks. *M. brevicaudata* was originally described as *Didelphis brevicaudatus* Erxleben, 1777. In the same year, Schreber, 1777 described *Didelphis brachyuros*. Both descriptions were based on the description and illustration of "*Muris sylvestris Americani faemina*" from Seba, 1734. Thomas, 1888 gave priority to Erxleben's name, considering *Didelphis brachyuros* a junior synonym. The specimen from Seba (BM 67.4.12.540) exhibit pelage "distinctly bicolored, reddish dorsally and abruptly paler ventrally", as quoted by Voss *et al.*, 2001 who analyzed the type specimen`s skin and confirmed the association of Erxleben`s, and Schreber`s names to it. Synonimyzing *surinamensis* Zimmermann, 1780 and *sebae* Gray, 1827 *with brevicaudata* is justified because the former two names were also created based on Seba`s specimen/ illustration, being objective synonymies of *M. brevicaudata*. The descriptions of "[*Didelphys*] *Hunteri*" and "*Peramys brevicaudatus dorsalis*" were based on specimens that fit our definition of *M. brevicaudata*, and are therefore junior synonymies. The type of "*Peramys brevicaudatus orinoci*" does not fit exactly our morphologic definition of *Monodelphis brevicaudata*, because it posses the middorsal stripe more grizzled, broader at head, the flanks lighter, and a smaller size than any specimen recognized by us as *M. brevicaudata*. However, because we do not know all morphological variation within *M. brevicaudata*, and considerable variation regarding the middorsal srtipe and size is obviously possible in this species (see the Geographic variation topic above), we provisionally consider *oriconi* as synonym of *brevicaudata*.

The restriction of the name *M. brevicaudata* herein proposed is supported by the morphological similarity between the specimen ROM 98909 (placed in our northwestern clade) and the type specimen of *M. brevicaudata*, both exhibiting homogeneously reddish dorsal fur, without a middorsal stripe. Our genetic samples from Venezuela and northern Guyana, which include localities close to the type locality of *M. brevicaudata* (Kartabo, north Guyana), grouped and formed a monophyletic lineage in the molecular analyses, highly divergent from any other. It is important to note that this clade includes both bicolored (ROM 98909) and tricolored specimens (L-1917, L-1920, USNM 568009), showing that the color of the dorsal pelage is a variable feature of this species (see Geographic variation above).

Monodelphis touan (Shaw, 1800)

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Type information. Holotype lost, from "Cayenne", French Guiana. Neotype FMNH 21720, designated by Voss *et al.*, 2001, an adult male from Cayenne, preserved as skin and skull. Collected by S. Klages on 26 February 1917.

Synonyms. *tricolor* Geoffroy, 1803.

Morphological Diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 137 mm in adult females and 159 mm in adult males. Dorsal pelage always with two distinct colors: a grizzled, gray colored stripe at middorsum, contrasting with reddish sides (Figure 4); head pelage reddish laterally, with middorsal stripe narrow, sometimes ill-defined, confined by a band of red hairs above each eye; underparts grayish cream, sharply differentiated from the reddish sides (Figure 5); throat and chin distinctly reddish; tail dorsally covered with body fur to about one third of the caudal length; ventrally, this coverage is shorter, limited to the tail`s connection with the body. CBL averages 35.5 mm in adult females and 39.8 mm in adult males; interorbital region relatively narrow (Figure 6); zygomatic arches slightly convergent anteriorly; UMS averages 7.8 mm in adult females and 8.0 mm in adult males.

Distribution. Found in northeastern South America, from French Guiana to the Brazilian state of Amapá (Figure 8).

Geographic variation. The extension of body fur on the dorsal surface of the tail corresponds to about one third of caudal length in specimens from Amapá, and to about one half of caudal length in specimens from French Guiana. Specimens from Amapá also have longer skulls when compared to French Guianan specimens, which show proportionally broader skulls.

Remarks. Based on Buffon, 1789 description of "*Le Touan*", with type locality in Cayenne, French Guiana, Shaw, 1800 described *Viverra touan.* Shaw noted the presence of a longitudinal dorsal gray fur in contrast to the lateral fur, being the first reference to a tricolor specimen of the *M. brevicaudata* group. In 1803, Geoffroy described *Didelphis tricolor* based also in a tricolor specimen from Cayenne (MNHN 1990.421). Until now, *D. tricolor* is regarded as a synonym of *M. brevicaudata* (e.g. Cabrera, 1919; Gardner, 2005; Pine & Handley, 2007; Thomas, 1888). Our new taxonomic arrangement, however, implies that *D. tricolor* should be considered a synonym of *M. touan.*

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Linares, 1998 also considered *M. touan* as a valid species, but applied the name *touan* to bicolored specimens, and the name *brevicaudata* to tricolored specimens. This application is inverted, as already noted by Voss *et al.*, 2001, because the pelage of the types of *brevicaudata* and *touan* are bicolored and tricolored respectively. Linares, 1998 considered that these forms occur in simpatry in eastern Venezuela, Guianas, and in the Brazilian state of Pará, and described craniodental characters supposedly useful to discriminate them. However, like Voss *et al.*, 2001, we did not find either evidences that any forms of the *brevicaudata* complex occur in simpatry in those regions, or consistent craniodental characters to separate them. Linares, 1998 also considered *touan* and *emiliae* as conspecific, but our morphological and molecular (see Figure 2) analyses do not support their conclusions.

The association of the name *M. touan* to specimens from French Guiana and Amapá is explained by the morphological similarity of the neotype of *Viverra touan* (FMNH 21720) with those specimens, all of them included in the east clade of our molecular analyses. The east clade showed considerable genetic divergence from the *M. brevicaudata* (strict sense) clade, allied to a remarkable morphological differentiation. Although the specimens considered by us as *M. touan* did not form a monophyletic clade with current data available(Figure 2), their paraphyly is not well supported either, and they are readily distinguishable on the basis of external morphology from the other specimens within the east clade (the ones from south of the Amazon river). The problem concerning the non monophyly of *M. touan* is further discussed below.

Monodelphis glirina (Wagner, 1842)

Type information. Holotype not cited in original description. Type locality "Mamoré", Rondônia, Brazil. "Rio Mamoré, Cachoeira da Pau grande" according to Pelzeln (1883), 10° 28'S $65^{o}24'W$ (Vanzolini 1993). Collected by Johann Natterer. The type specimen is possibly at the Naturhistorisches Museum Wien (NMW), where part of Natterer's collection can be found.

Synonyms. *maraxina* Thomas, 1923.

Morphological Diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 137 in adult females and 153 in adult males. Dorsal pelage commonly with two colors: a grizzled, light gray colored stripe at middorsum, differing from the light orange to orange sides (Figure 4). Specimens from east of the Xingu river (Canaã dos Carajás, Marabá, São Félix do Xingu, São João do Araguaia) lack the middorsal stripe; instead,

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they exhibit upperparts grayish, with lateral orange fur restricted either to the contact line between anterior body sides and venter or to head sides; head pelage orange laterally and grayish dorsally, with the middorsal stripe broad, occupying all crown of the head between the eyes; underparts grayish cream to grayish light-orange, not sharply differentiated from the orange sides (Figure 5); throat commonly slightly more washed with orange than the rest of the venter; Mammae at the inguinal/abdominal region, one central and eight distributed circumferentially around it (MPEG 1318, 10134, 38985, 39115, 39140); tail covered with body fur to about the same extent above and below (up to one-sixth of the caudal length). CBL averages 36.5 mm in adult females and 39.4 mm in adult males (Table 2); interorbital region relatively narrow (Figure 6); zygomatic arches slightly rounded anteriorly; maxillopalatine foramina proportionally longer (Figure 7); UMS averages 8.1 mm in adult females and 8.2 mm in adult males.

Distribution. Southeastern Peru, northern Bolivia and western Brazil in the states of Acre, Rondônia and southern Amazonas, trough north of Mato Grosso and Pará south of Rio Amazonas, including localities east of Rio Xingu (Figure 8).

Geographic variation. *M. glirina* exhibits high morphological variation, mainly in the body pelage color. As mentioned before, specimens from east of the Xingu river have no middorsal stripe. Additionally, although most specimens of *M. glirina* have grayish yellow ventral pelage, with gray-based and yellowish-tipped hairs, specimens from Marabá, Pará, on east of the Xingu river, exhibit notably darker ventral fur (gray colored). Another specimen from east of the Xingu river (MPEG 10134, São João do Araguaia, Pará) shares with other specimens from this region the absence of a distinct stripe at middorsum, but exhibits brownish orange (instead of grayish) upper fur, and underparts grayish to light-orange, similar to the underparts of specimens from Altamira and Santarém (both in Pará), on the west margin of the Xingu river.

Specimens from the state of Mato Grosso are generally more grayish and paler, with the grey colored middorsal stripe wider, and orange fur on body sides proportionally lighter and narrower, restricted to the area adjacent to the venter (commonly not so restricted as in specimens from east of the Xingu river). In many specimens the orange fur of body sides becomes gradually narrower toward the back, with posterior part of the body gray colored instead of orange. The venter is yellowish, with hairs gray based.

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Specimens from Altamira, Itaituba, and Santarém, in state of Pará, are brighter orange on the flanks, with the middorsal stripe generally narrower and well delimited. The venter is more washed with orange than in specimens from the state of Mato Grosso. Specimens from Vitória do Xingu, Pará are the most brightly colored, with rich orange flanks, and darker middorsal stripe and venter. Specimens from Santa Rosa, Bolivia resemble those from Altamira, Itaituba and Santarém regarding dorsal and lateral pelage, but show more grayish ventral pelage. The two skins from Fazenda Vilhena, state of Rondônia, and the only one from state of Acre, closely resemble specimens from Santa Rosa, Bolívia, whereas specimens from Humaitá (Amazonas), Santa Bárbara and Campo Novo de Rondônia, also in Rondônia are more similar to specimens from Mato Grosso.

Remarks. The color pattern observed in specimens of *M. glirina* from east bank of the Xingu river show a striking concordance with the original description of *M. maraxina* by Thomas, 1923, a species considered to be restricted to Marajó Island, state of Pará. Thomas, 1923 suggested that *M. maraxina* is closely related to *M. domestica*. Subsequent authors agreed with him, some of which even regarded *M. maraxina* as synonym of *M. domestica* (e.g. Cabrera, 1958; Emmons & Feer, 1990; Emmons & Feer, 1997). However, Pine, 1980 suggested that a relationship of *M. maraxina* with members of the brevicaudata group (which excludes *M. domestica* in his view) would be more reasonable on zoogeographic grounds. Additionally, the relative hairlessness of the tail and the buffy coloration of body sides are conditions shared with specimens of *M. brevicaudata* from the east bank of the Tapajós river (=*M. glirina*).

Although we have not performed direct analyses of any specimen regarded as *M. maraxina*, the analysis of *M. maraxina* holotype (BMNH 12.5.11.13) through photographs confirmed that it posses skin and skull highly similar to the ones exhibited by specimens of *M. glirina* from east of the Xingu river. Similarities between the faunas of the Marajó Island and the adjacent region of the east margin of the Xingu river are expected, as indicated by other vertebrate groups (e.g. Avila-Pires, 1995; Fernandes, Cardoso da Silva & Silva Jr, 1995; Nascimento *et al.*, 1991; Ron, 2000). Furthermore, our recent field work at Marajó resulted in specimens of another species of the brevicaudata complex that is also present on the east margin of the Xingu river (*M*. sp. nov. "touan sul"), confirming that these areas are able to share species of short-tailed opossum.

Given the substantial morphological similarity between the holotype of *M. maraxina* and the specimens from east of the Xingu river, which actually are geographic variants of *M. glirina* (see molecular analyses results above), and the evidences that these areas are able to share

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species of short-tailed opossum, we argue that *M. maraxina* is a junior synonym of *M. glirina*. However, since our general analyses are not conclusive in respect to *M. glirina*, which may represent a complex of species rather than an unique species, it is possible that the assignment of *M. maraxina* to *M. glirina* will change as more accurate analyses based on more molecular sequences and geographic samples are available for *M. glirina*.

Monodelphis palliolata (Osgood, 1914)

Type information. Holotype FMNH 20524, an adult male from "San Juan de Colon, state of Tachira, Venezuela", 2.500 ft. elevation. Collected by M. P. Anderson on 14 Nov. 1913. Preserved as skin and skull.

Morphological diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 127 mm in adult females and 152 mm in adult males (Table 2). Dorsal pelage always with two distinct colors: a grizzled, gray colored stripe at middorsum, differing from the orange sides (Figure 4); head pelage orange laterally and grayish dorsally, with the middorsal stripe broad, occupying all crown of the head between the eyes; underparts grayish light-orange to grayish orange, not sharply differentiated from the orange sides (Figure 5); throat slightly more washed with orange than the rest of the venter; tail covered with body fur to about the same extent (one-fifth of caudal length) on dorsal and ventral sides. CBL averages 34.2 mm in adult females and 38.4 mm in adult males (Table 2); interorbital region relatively broad (Figure 6); zygomatic arches sharper convergent anteriorly; maxillopalatine foramina proportionally longer (Figure 7); UMS averages 7.5 mm in adult females and 7.6 mm in adult males.

Distribution. West of Rio Orinoco in northern Venezuela and northeastern Colombia (Figure 8; the Colombian records of *M. palliolata* have no specific localities identified – see Pine & Handley, 2007 –, and are not plotted in the map).

Geagraphic variation. *M. palliolata* was not thoroughly investigated regarding the geographic variation, and our localities do not cover completely the known geographic distribution of this species. Specimens examined showed no high external and cranial variation, being relatively more conservative than other species studied. Although no geographical correlation was investigated, some variable features include the extension of the body fur onto the tail (one-fourth to about one-sixth of tail`s length), the color intensity of the lateral body fur (orange to

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bright orange, tending to reddish), the shade of the ventral fur (light to rich orange), and the shade of the middorsal fur (light to rich gray).

Remarks. Osgood, 1914 described the species *Peramys palliolatus* and cited that it differs from *P. brevicaudatus* (= *Monodelphis brevicaudata*) by the more richly tawny color of under parts, and the less extensive hairiness of the upper side of the tail. Many subsequent studies considered *palliolata* as a subspecies of *M. brevicaudata* (e.g. Cabrera, 1958; Pérez-Hernández, 1989; Pérez-Hernández, Soriano & Lew, 1994; Ventura *et al.*, 1998) or its junior synonym (Gardner, 1993). Voss *et al.*, 2001 considered *M. palliolata* a valid species, which can be readily distinguished from *M. brevicaudata* by external features. Based on studies of skull morphometrics, Lew *et al.*, 2005 also supported the recognition of *palliolata* as a distinct species. To date, the specific status of *palliolata* is consensual among mammalogists (Gardner, 2005; Pine & Handley, 2007). Here, we emphasize that *M. palliolata* is a distinct species, reaffirming diagnostic features used by Voss *et al.*, 2001, adding some cranial features that are helpful in distinguishing it from *M. brevicaudata* and *M. glirina* (see Morphological Comparisons below).

Monodelphis "touan sul", new species

Fig. 9A

Holotype. an adult male to be deposited at MPEG, collected between Jan to Jun 2007 by M. A. Ribeiro-Júnior (field number MAR 880), at Igarapé Caquajó, Floresta Nacional de Caxiuanã, Portel, Pará, Brazil, -1° 57' 50'' S -51° 37' W, elevation 45 m. The holotype consists of skin, skull, and liver tissue fixed in ethanol.

Paratypes. Five aduld males, three adult females and two juveniles to be deposited at MPEG, MN, MZUSP, and UFMG, collected between Jan to Jun 2007 by M. A. Ribeiro-Júnior (field numbers MAR 159, 200, 422, 427, 1023, 1200, 1312, 272, 375, 1205, 218, 872), from the type locality, consisting of skin, skull, and liver tissue fixed in ethanol; one adult male and two juvenile males to be deposited at MPEG, collected on Sep 2007 by J. Gomes (field number CAX 602, 630, 645), from the type locality, consisting of ethanol preserved specimens.

Diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 155 mm in adult males. Dorsal pelage with clearly two distinct colors: a grizzled, blackish gray colored stripe at middorsum, contrasting with reddish sides (Figure 4, 9A); head

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pelage reddish laterally, with middorsal stripe broad, occupying the entire or almost the entire crown of the head between the eyes; underparts grayish cream, sharply differentiated from the reddish sides (Figure 5); throat and chin distinctly reddish; tail covered dorsally with body fur to about one-fifth of caudal length; ventrally, this coverage is limited to the tail`s connection with the body. CBL averages 36.7 mm in adult females and 39.8 mm in adult males (Table 2); interorbital region relatively narrow (Figure 6); zygomatic arches slightly convergent anteriorly; UMS averages 8.2 mm in adult females and 8.2 mm in adult males (Table 2).

Description based on the holotype and paratypes.

Dorsal and lateral pelage. Dorsal body pelage grizzled, with dark gray middorsum contrasting with reddish flanks, therefore forming a well defined stripe from the nose to the base of the tail (Figure 4), becoming red-washed on the rump, mainly in older specimens. Cover hairs of middorsal fur ca. 8 mm-long at shoulders, dark gray basally (brown at the base, darker toward the tip) and whitish distally (ca. 1mm), turning blackish at the tip. Guard hairs sparser, longer (ca. 10 mm), slightly coarser than cover hairs, entirely dark brown or black. At head, middorsal stripe occupies the entire crown between the eyes. Lateral fur bright red colored, with hairs grayish brown basally, gradually turning darker to the middle, and reddish distally. Next to the ears the red portion of the lateral hairs becomes proportionally longer, resulting in a fur almost entirely reddish.

Ventral pelage. Ventral fur grayish basally and yellowish cream distally, clearly distinct from the lateral fur in color (Figure 5). Ventral hairs ca. 4 mm long, whitish at the base, becoming dark brown to blackish toward the middle, and cream distally. Very few hairs entirely cream or entirely gray are also present. Hairs become gradually shorter and red-washed from the chest toward the chin. Some specimens exhibit reddish tipped hairs next to the base of the tail, showing the inguinal region reddish colored.

Vibrissae. Mystacial and genal vibrissae blackish, except for a few shorter ones that are light colored in the two series. The longest mystacial vibrissae generally extend beyond eyes when laid flat against cheek, but do not reach the base of pinnae. The genal vibrissae generally reach pinnae and frequently do not extend beyond its posterior border. There is one pair of supraorbital vibrissae, blackish and unequal in size. There are few (up to four) submental and interramal vibrissae, that varies from whitish to light brown colored. Vibrissae are also present on the dorsal surface of forearm close to the elbow (one or two sparsed hairs), and on the ventral surface of forearm close to the manus (one to three hairs); both vibrissae arrays have

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hairs turned to the sides, unequal in size, and color varing from whitish to brownish, frequently darker basally and lighter toward the tips.

Limbs. Dorsal pelage of legs and arms as colored as the lateral body pelage; ventral pelage of legs and arms colored as the ventral body pelage. Hands and feet dark brownish gray to blackish in general aspect. Hairs on metacarpals and metatarsal generally brown basally and cream to yellowish distally, but there are some ones brown, cream or yellowish self-colored. Digits dorsally covered with short, dark brown to blackish hairs. Ungual tufts blackish, sparse and short, reaching approximately the middle of the claws on hands and almost the tips of the claws on feet. Hands and feet with digit III slightly longer than digits II and IV, the latter two subequal in size. Digits I and V shorter than digits II-IV. On feet, the digit V reaches about 2/3 of the digit IV length, and the hallux reaches about the base of digit II. Plantar surface hairless, covered with five enlarged convex tubercles: the thenar pad and four interdigitals pads; the former is the longest, and the latter are proportionally wider, of which the first interdigital pad is commonly the longest.

Tail. Tail short, a little longer than one half of the head and body`s length. Body fur covers the dorsal surface of the tail to about one fifth of caudal length. This coverage fur is reddish gray colored, and gradually becomes sparser and shorter toward the tail tip. The uncovered part of the tail is bicolor (blackish dorsally and grayish/brownish ventrally). Tail scales are small, blackish, and rectangular in shape, each one bearing three hairs.

Other external features. Ears small, uniformly blackish, hairless without magnification, but covered internally and externally with very short and thin hairs, that appear whitish above the blackish surface of the ears. Mammary formula unknown. Scrotal skin blackish, covered with yellowish cream hairs.

Skull. Skull relatively large for the genus (Table 2), with braincase shorter than rostrum (Figure 6).

Rostrum. Rostrum gently concave in dorsal view at premolars line, especially at Pm2. Infraorbital foramen enlarged. Nasals narrow and parallel anteriorly, becoming gradually wider posteriorly until reaches the greatest width at the frontal/maxillary suture, and then gradually narrowing toward the posterior end; the shape of the posterior end is generally round. Premaxillary extends anteriorly slightly beyond the first upper incisive, not forming a distinct rostral process.

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Orbital region. Lacrimal foramen consisted of two openings located at the anterior edge of orbits, externally to the orbital cavity. A third smaller, anteriorly directed foramen is located in the orbital process of the lacrimal. This last opening may be absent on one or both sides. Interorbital region moderately constricted, hourglass shaped. Supraorbital crests absent, with crown elements and orbital elements conected in a smooth curvature. Zygomatic arches robust, slightly convergent anteriorly.

Braincase. Sagital crest weak, more evident in older adult males. Temporal lines weak or absent. Interparietals almost reaching the squamosal laterally (reach in the specimens MAR 127, 1023, left side), hat-shaped, with the medial portion broader, becoming gradually narrower toward laterals. Nuchal crests well defined and developed, with the lateral expansions merging with enlarged posttympanic processes of the esquamosal. Excoccipitals not joined, and dorsal margin of foramen magnum formed by exoccipitals and supra-occipital.

Palate. Incisive foramen short, extending anteriorly until the third or the anterior margin of the fourth upper incisive, and posteriorly until the upper canine. Maxillopalatine fenestra aproximatelly twice as long as the incisive foramen, extending from the first upper molars to the third upper molars. Posterolateral palatal foramen relatively large, as long as one half of the incisive foramen length, oval shaped, located immediately behind the fourth molar, with anterior border reaching about the posterior line of M4 in adult specimens. Maxillary and palatine fenestra absent, but some diminute perforations are present on the palatine. Palatine inflected ventrally, with approximately straight posterior edge.

Basicranium. Roof of the nasopharyngeal passage not perforated by vacuities. Alisphenoid bone with a distinct infratemporal longitudinal crest, which marks the ventral limit of the attachment of the temporalis muscle (see Wible, 2003). Bulla usually extending ventrally beyond the occipital condyle. Occipital condyle extending ventrally beyond the small and rounded parocciptal process. Alisphenoid tympanic process moderately inflated, rounded, slightly wider than longer. Ectotympanic about twice longer than wider. Anteromedial surface of the tympanic process of the alisphenoid pointed or rounded, but without a bony strut or lamina connecting it with the transverse canal foramen. Promontorium well developed, with an elongated rostral tympanic process of the petrosal.

Mandibles. Mandibular rami shallow and bowed, but robust. Mandible with two mental foramina, the anterior between pm1 and pm2 or below pm2, and the posterior below m1 or between m1 and m2. Coronoid process high and wide, three times higher than the ramus.

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Mandibular condyle rounded laterally, extending posteriorly beyond the broader coronoid process. Angular process acute and inflected medially. Posterior shelf of masseteric fossa robust.

Teeth. First upper incisor styliform, hypsodont, separated from I2–I5 by a short diastema. I2-I5 subequal in size, but with crowns showing a tendency of becoming wider from I2 to I5. Upper canines large and robust, at least twice as high as Pm1 in females and young adult males, and three times higher than Pm1 in adult male specimens. Pm1 about one half the size of Pm2, separated from the latter by a very small gap, absent in a few specimens. Pm2 and Pm3 subequal in size, but Pm3 slightly higher than Pm2, and Pm2 proportionally wider, with posterior cutting edges more developed than in Pm3. Upper molars large, increasing in breadth from M1 to M4, all of them with well-developed anterior cingulum. Lower incisors similar in size, with lingual cusp present, and spoon-shaped in ventral view. Commonly, there is a small gap between pm1 and pm2. Second and third lower premolars subequal in height, but pm2 wider and with posterior cutting edges more developed than pm3.

Geographic distribution. Found in the Brazilian state of Pará south of Rio Amazonas and east of Rio Xingu, including Ilha de Marajó (Figure 8).

Geographic variation. Specimens from Portel are especially dark, showing the stripe at middorsum dark gray to blackish, tail and ears black. On the other hand, specimens from São Geraldo do Araguaia and from the localities "near Itupiranga" and "near Jatobal", in Marabá have stripe at middorsum lighter (gray colored instead dark-gray) and laterals much light red when compared to the others specimens of *M.* sp. nov. "touan sul". Also, they show middorsal stripe slightly narrow on the head, with a thin line of red hairs above each eye. Specimens from Anapu and Floresta Nacional de Tapirapé Aquiri, in Marabá, are similar to specimens from Caxiuanã, but some ones have the middorsal stripe narrower on the head, similar to specimens from near Itupiranga and Jatobal, and from São Geraldo do Araguaia. In general, specimens from Portel, Altamira, Cametá, and Porto de Moz have larger and more robust skull than specimens from São Geraldo do Araguaia and from near Itupiranga and Jatobal.

Remarks. This form was previously cited by Carvalho, 1962 as *Monodelphis brevicaudata emiliae*; by Gomes, 1991 as *Monodelphis* sp.1; by Voss *et al.*, 2001 as an unnamed form; and by Pine & Handley, 2007 as *Monodelphis* species D (Figure 2).

Monodelphis **"Trombetas", new species**

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Fig. 9B

Holotype. MPEG 38052, an adult male collected on 17 May 2006 by B. A. Costa (field number BAC 204), at Platô Greig, 43 Km SW Porto Trombetas, Oriximiná, Pará, Brazil, -1° 49' 43'' S -56° 25' 02'' W, elevation 160 m. The holotype consists of skin, skull, and liver tissue fixed in ethanol.

Paratypes. MPEG 38054, 38095, 38056, 38074, two adult males and two adult females collected on May 2006, two juvenile males and two adult males to be deposited at UFMG, collected on Aug 2006, all collected by B. A. Costa (field numbers BAC 164, 202, 166, 169, BAC 228, 229, 236, 237), from the type locality, consisting of skin, skull, and liver tissue fixed in ethanol, except by MPEG 38095 and 38074, which consist of ethanol conserved specimens; MPEG 38063, an adult male collected on May 2006, an adult male and a subadult female to be deposited at UFMG, collected on Aug 2006, all collected by B. A. Costa, (field numbers BAC 177, 231, 233), at Platô Teófilo, Porto Trombetas, Oriximiná, Pará, Brazil, -1° 45' 60'' S -56° 34' 16'' W, elevation 176 m, consisting of skin, skull, and liver tissue fixed in ethanol; MPEG 38093, an adult male collected on May 2006, a juvenile female to be deposited at UFMG, collected on Aug 2006, both collected by B. A. Costa (field numbers BAC 201, 230), at Platô Bela Cruz, 40 Km SW Porto Trombetas, Oriximiná, Pará, Brazil, -1° 48' 09'' S -56° 30' 30'' W, elevation 176 m, the first one consisting of ethanol conserved specimen, and the last one consisting of skin, skull, and liver tissue fixed in ethanol; MPEG 39810, a juvenile female collected on May 2007 by L. G. Vieira (field number LGV 146), at Platô Cipó, 60 Km S Porto Trombetas, Oriximiná, Pará, Brazil, -1° 44' 03'' S -56° 36' 42'' W, elevation 160 m, consisting of skin and liver tissue fixed in ethanol; MPEG 39811, 39812, an adult male and a juvenile male collected on May 2007 by Leonardo G. Vieira (field numbers LGV 148, 149), at Igarapé Greig, ca. 60 Km SW Porto Trombetas, Oriximiná, Pará, Brazil, -1° 50' 26'' S -56° 31' 31'' W, elevation 160 m, consisting of skin and liver tissue fixed in ethanol; a juvenile female and a juvenile male to be deposited at UFMG, collected on May 2007, two adult males and a juvenile female to be deposited at UFMG, collected on Nov 2007, all collected by S. L. Freitas, (field numbers SLF 216, 244, 325, 335, 337), at Platô Bacaba, Porto Trombetas, Oriximiná, Pará, Brazil, -1° 46' 11'' S -56° 22' 09'' W, elevation 160 m, consisting of skin, skull, and liver tissue fixed in ethanol.

Diagnosis. Same as the general for the *M. brevicaudata* complex with the following additions: HBL averages 133 in adult females and 149 in adult males. Dorsal pelage with clearly two distinct colors: a grizzled, gray colored stripe at middorsum, contrasting with reddish sides (Figure 4, 9B); head pelage reddish laterally, with narrow middorsal stripe, commonly ill-

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defined and sometimes almost indistinct, confined middorsally by a band of red hairs above each eye; underparts grayish cream to yellowish, sharply differentiated from the reddish sides (Figure 5); throat and chin distinctly reddish; tail covered dorsally with body fur up to about one third of caudal length; ventrally, this coverage is limited to the tail`s connection with the body. CBL averages 35.0 mm in adult females and 38.5 mm in adult males (Table 2); interorbital region relatively narrow (Figure 6); zygomatic arches slightly convergent anteriorly; UMS averages 7.7 mm in adult females and 7.9 mm in adult males (Table 2).

Description based on holotype and paratypes.

Dorsal and lateral pelage. Dorsal body pelage grizzled, with gray middorsum contrasting with reddish flanks, therefore forming a well defined stripe from the ears to the base of the tail (Figure 4), becoming red-washed on the rump, mainly in older specimens. Cover hairs of middorsal fur ca. 8 mm-long at shoulders, gray basally (light brown at the base, darker toward the tip) and whitish distally (ca. 1mm), turning dark brown or black at the tip. Guard hairs sparser, longer (ca. 10 mm), slightly coarser than cover hairs, entirely dark brown or black. At head, middorsal stripe is narrow and light colored, commonly light grey to whitish buff, ill-defined, confined middorsally by a band of red hairs above each eye, giving a general reddish aspect to the head. Some specimens show the band of red fur above each eye wider, and the stripe is reduced to a line. Lateral fur bright red colored, with hairs grayish brown basally, gradually turning darker to the middle, and reddish distally. Next to the ears the red portion of the hairs becomes proportionally longer, resulting in a fur almost entirely or entirely reddish.

Ventral pelage. Ventral fur grayish basally and yellowish cream distally, clearly distinct from the lateral fur in color (Figure 5). Ventral hairs ca. 4 mm long, whitish at the base, becoming brownish toward the middle, and yellowish cream distally. Some hairs entirely cream or entirely gray are also present. Hairs became gradually shorter and red-washed from the chest toward the chin. Some specimens exhibit reddish tipped hairs next to the base of the tail, showing the inguinal region reddish colored.

Vibrissae. Mystacial and genal vibrissae blackish, except for a few shorter ones that are light colored in the two series. The longest mystacial vibrissae generally extend beyond eyes when laid flat against cheek, but do not reach the base of pinnae. The genal vibrissae generally reach pinnae and frequently do not extend beyond its posterior border. There is one pair of supraorbital vibrissae, blackish and unequal in size. There are few (up to five) submental and interramal vibrissae, that varies from whitish to light brown colored. Vibrissae are also present

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on the dorsal surface of forearm close to the elbow (one or two sparsed hairs), and on the ventral surface of forearm close to the manus (one to three hairs); both vibrissae arrays have hairs turned to the sides, unequal in size, and color varing from whitish to brownish, frequently darker basally and lighter toward the tips.

Limbs. Dorsal pelage of legs and arms as colored as the lateral body pelage; ventral pelage of legs and arms as colored as the ventral body pelage. Hands and feet brownish gray in general aspect. Hairs on metacarpals and metatarsal generally brown basally and yellowish to orange distally, but there are some ones brown, yellowish or orange self-colored. Digits dorsally covered with short brownish hairs. Ungual tufts brownish to golden-brown, sparse and short, reaching approximately the middle of the claws on hands and almost the tips of the claws on feet. Hands and feet with digit III slightly longer than digits II and IV, the latter two subequal in size. Digits I and V shorter than digits II-IV. On feet, the digit V reaches about 2/3 of the digit IV length, and the hallux reaches about the base of digit II. Plantar surface hairless, covered with five enlarged convex tubercles: the thenar pad and four interdigitals pads; the former is the longest, and the latter are proportionally wider, of which the fourth interdigital pad is commonly the longest.

Tail. Tail short, a little longer than one half of the head and body`s length. Body fur covers the dorsal surface of the tail to about one third of caudal length. This coverage fur is reddish colored, and gradually becomes sparser and shorter toward the tail tip. The uncovered part of the tail is weakly bicolor (brownish dorsally and lighter brown ventrally). Tail scales are small, brownish, and rectangular in shape, each one bearing three hairs, the central one generally darker and slighter thicker.

Other external features. Ears small, uniformly brownish, hairless without magnification, but covered internally and externally with very short and thin hairs, brownish or golden colored. Scrotal skin brownish, covered with yellowish cream hairs.

Skull. Skull relatively large for the genus (Table 2), with braincase shorter than rostrum (Figure 6).

Rostrum. Rostrum gently concave in dorsal view at premolars line, especially at Pm2. Infraorbital foramen enlarged. Nasals narrow and parallel anteriorly, becoming gradually wider posteriorly until reaches the greatest width at the frontal/maxillary suture, and then gradually narrowing toward the posterior end; the shape of the posterior end is generally round.

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Premaxillary extends anteriorly slightly beyond the first upper incisive, not forming a distinct rostral process.

Orbital region. Lacrimal foramen consisted of two openings located at the anterior edge of orbits, externally to the orbital cavity. A third smaller, anteriorly directed foramen is located in the orbital process of the lacrimal. This last opening may be absent on one or both sides. Interorbital region moderately constricted, hourglass shaped. Supraorbital crests absent, with crown elements and orbital elements conected in a smooth curvature. Zygomatic arches robust, slightly convergent anteriorly, more expanded to laterals on males than in females, and commonly more expanded in older specimens.

Braincase. Sagital crest evident in males and weak in female. Temporal lines weak in males and indistinguishable in females. Interparietals almost reaching the squamosal laterally (reach in specimen BAC 237, left side), hat-shaped, with the medial portion broader, becoming gradually narrower toward laterals. Nuchal crests well defined and developed, with the lateral expansions merging with enlarged posttympanic processes of the esquamosal. Excoccipitals not joined, and dorsal margin of foramen magnum formed by exoccipitals and supra-occipital.

Palate. Incisive foramen short, extending anteriorly until the fourth or posterior line of the third upper incisive, and posteriorly until the upper canine (Figure 7). Maxillopalatine fenestra aproximatelly twice as long as the incisive foramen, extending from the first upper molars to the third upper molars. Posterolateral palatal foramen relatively large, as long as one half of the incisive foramen length, oval shaped, located immediately behind the fourth molar, with anterior border reaching about the posterior line of M4 in adult specimens. Maxillary and palatine fenestra absent, but some diminute perforations are present on the palatine. Palatine inflected ventrally, with approximately straight posterior edge.

Basicranium. Roof of the nasopharyngeal passage not perforated by vacuities. Alisphenoid bone with a distinct infratemporal longitudinal crest, which marks the ventral limit of the attachment of the temporalis muscle (see Wible, 2003). Bulla usually extending ventrally beyond the occipital condyle. Occipital condyle extending ventrally beyond the small and rounded parocciptal process. Alisphenoid tympanic process moderately inflated, rounded, slighter wider than longer. Ectotympanic about twice longer than wider. Anteromedial surface of the tympanic process of the alisphenoid pointed or rounded, but without a bony strut or lamina connecting it with the transverse canal foramen. Promontorium well developed, with an elongated rostral tympanic process of the petrosal.

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Mandibles. Mandibular rami shallow and bowed, but robust. Mandible with two mental foramina, the anterior between pm1 and pm2 or below pm2, and the posterior below m1 or between m1 and m2. Coronoid process high and wide, three times higher than the ramus. Mandibular condyle rounded laterally, extending posteriorly beyond the broader coronoid process. Angular process acute and inflected medially. Posterior shelf of masseteric fossa robust.

Teeth. First upper incisor styliform, hypsodont, separated from I2–I5 by a short diastema. I2-I5 subequal in size, but with crowns showing a tendency of becoming wider from I2 to I5. Upper canines large and robust, at least twice as high as Pm1 in females and young adult males, and at least three times higher than Pm1 (commonly more) in adult male specimens. Pm1 about one half the size of Pm2, separated from the latter by a very small gap, absent in the specimen BAC 164. Pm2 and Pm3 subequal in size, but Pm3 slightly higher than Pm2, and Pm2 proportionally wider, with posterior cutting edges more developed than in Pm3. Upper molars large, increasing in breadth from M1 to M4, all of them with well-developed anterior cingulum. Lower incisors similar in size, with lingual cusp present, and spoon-shaped in ventral view. Commonly, there is a small gap between pm1 and pm2. Second and third lower premolars subequal in height, with p2 commonly slightly taller (specimen BAC 237, however, show p3 clearly taller than p2), but pm2 wider and with posterior cutting edges more developed than pm3.

Geographic distribution. Center-South Guyana, Suriname, and Brazil in the southeastern of state of Roraima, east of state of Amazonas (north of Rio Amazonas) and center-west of state of Pará (north of Rio Amazonas) (Figure 8).

Geographic variation. *M.* sp. nov. "Trombetas" shows the extension of the body fur onto the tail and the tonality of the dorsal, ventral and lateral coloration quite variable. The analysed specimens from Cachoeira Porteira, Oriximiná (Pará, Brazil) have a longer proportion of the tail covered by body hairs (one third or slightly more) than specimens from Porto Trombetas, also in Oriximiná, Faro (Pará, Brazil) and Alenquer (Pará, Brazil) (one third or slightly less). Specimens from these three last localities show the grayish base of the venter more evident than specimens from Cachoeira Porteira. Specimens from Tiriós (Pará, Brazil), Brokopondo and Sipaliwini (Surinam) are more similar to specimens from Cachoeira Porteira. Specimens from Potaro-Siparuni (Guyana) have about a half of the tail length covered by body fur, and the venter more grayish than the all other of this species. One specimen from Potaro-Siparuni (ROM 108477) shows the middorsal stripe less contrasting with laterals than commonly in this

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species. Specimens from Manaus and Itacoatiara (Amazonas, Brazil) appears smaller than specimens from all other localities, show the underparts more yellowish, a more extensive coverage of the tail by body fur (at least a half, commonly more), and the middorsal fur with the grayish tonality lighter than average in this species, whitish or yellowish at head`s height. The specimen from Marowijne (Surinam) show the middorsal stripe too light along the body, less contrasting with laterals than all other specimens of this species, witish and almost indistinct at the crown. The tail is covered by body fur on more than a half of it`s lenght.

The skull showed a considerable variation inside this species, even between specimens of the same locality, sex and age class (individual variation). Specimens from Porto Trombetas do not showed the roof of nasopharyngeal passage perforated by vacuities, while in specimens from other localities this vacuities can be present, but is not commonly observed in complete adult specimens. In a other hand, in specimens from Manaus and Itacoatiara, these vacuities are present in all individuals (all adults), except in one exemplar (MN 16802). Cranially, specimens from these two municipalities have a smaller skull and zygomatic arches less expanded to laterals than average for this species.

Non geographic Variation

Sexual Dimorphism

All species herein studied exhibit sexual dimorphism in most external and craniodental dimensions (Table 2), with males averaging larger than females. Through direct analysis, we observed a clear sexual dimorphism in general size and robustness of the skull, size of upper canines, and development of cranial crests. Due to sample sizes we were able to test sexual dimorphism only in *M.* sp. nov. "Trombetas", for which we used specimens from Oriximiná and Faro, Pará, Brazil, and in *M. glirina*, from which we used specimens from Aripuanã, Mato Grosso, Brazil.

The two species tested showed to be sexually dimorfic. Males and females of *M.* sp. nov. "Trombetas" and *M. glirina* difered significanty (p≤ 0.05) in 15 and 14 craniodental measurements, respectively (Table 3). The 13 variables shared by both species as sexually dimorfic are associated to skull's length (GLS, CBL, RL, NL, PL, LM), breadth (BPG, BRC, BBC, ZB), and upper canine's development (HC, MTR, LTR). The 15 variables shared by both species as non-significant were exclusively related to incisive and molar teeth (LUI, LM3, WM3, WM4, LMS) or associated to the medial region of skull, which is apparently less or non related to

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skull`s size and robustness (PBM3, PPB, BFO, LTB, LIF, BIF, LMP, BMF, NB, POC). Additionally, the variables BRO and HMB were dimorfic only in *M.* sp. nov. "Trombetas", and the variable UMS was dimorfic only in *M. glirina*.

Sexual dimorphism has been reported in many Didelphid marsupials, including species of *Didelphis* (Cerqueira & Lemos, 2000; Gardner, 1973; Lemos & Cerqueira, 2002; Tyndale-Biscoe & Mackenzie, 1976), *Gracilinanus* (Freitas, 2007), *Marmosa* (López-Fuster *et al.*, 2002), *Marmosops* (Mustrangi & Patton, 1997), *Metachirus* (Vieira, 2006), *Philander* (Lew *et al.*, 2006), *Thylamys* (Carmignotto & Monfort, 2006) and *Monodelphis* (Pine, Dalby & Matson, 1985; Van Nievelt & Smith, 2005; Ventura *et al.*, 1998). Our results are in accordance with those of Pine *et al.*, 1985 for *Monodelphis dimidiata*, and Ventura *et al.*, 1998 for *M. brevicaudata* and *M. palliolata*, who also showed that males and females of these species are differentiated by general size and robustness of skull, but not by dental characters (except for the canine teeth, larger in males). Although we did not test sexual dimorphism in *M. brevicaudata*, *M. touan*, *M. palliolata*, and *M.* sp. nov. "touan sul", we believe they are also sexually dimorphic based on empirical data (Table 2) and on Ventura *et al.*, 1998.

Ontogenetic variation

Ontogenetic variation in skin was observed in all species studied. The direct observation of skins showed that juveniles are generally more grayish, mainly on ventral fur, and the distinction between the lateral and middorsal fur is weak, or even absent when the specimen is too young. Also, juvenile specimens show the tail less covered by body pelage than adults. Subadults and early adults show ventral fur more grayish than old adults, but have middorsal and lateral fur color similar to the adults.

Cranially, specimens appear to exhibit continuous growth even after reaching dental maturity. Ontogenetic variation in skull development was observed in both sexes. Regarding the ontogenetic variation tests, differences between the age classes 5 and 6 were assessed in males and females of *M. glirina*, and differences among age classes 6, 7, and 8 were assessed in both sexes of *M.* sp. nov. "Trombetas" and *M. glirina*, and in males of *M. palliolata*.

When age classe 5 (sample size= 10 to 13 males and 9 to 12 females) and age class 6 (sample size = 16 to 21 males and 22 to 27 females) specimens of *M. glirina* were compared, none variable was significantly different ($p \leq 0.05$) in females, and only two (GLS and CBL) were significantly distinct in males.

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Comparisons between age classes 6 and 7 showed the higher number of significantly distinct variables (Table 4). In females, *M.* sp. nov "Trombetas" and *M. glirina* exhibited respectively three and five distinct variables. In males, *M.* sp. nov "Trombetas", *M. glirina*, and *M. palliolata* exhibited respectively 12, 17, and eight distinct craniodental measurements.

When age classes 7 and 8 were statistically compared in females, none variable was significantly distinct in *M.* sp. nov "Trombetas", but five variables were distinct in *M. glirina* (Table 4). When these age classes were compared in males, *M.* sp. nov "Trombetas", *M. glirina*, and *M. palliolata* exhibited respectively two, 12, and seven distinct craniodental measurements (Table 4).

Similarly to the sexual variation on skull, the craniodental measurements that contribute more for the ontogenetic variation detected in this study are those related to general size and robustness of the skull such as GLS, CBL, PL, HC, BRC, BRO, ZB, and LM. The variables UMS and LMS, that are exclusively related to the molars and appear as significantly distinc between classes 7 and 8 in males of *M.* sp. nov "Trombetas", are exceptions, which can be explained by a reduction of tooth's crown in very old specimens.

Morphological comparisons

Most of the diagnostic characters found in the species of the *M. brevicaudata* complex are related to the external morphology (mainly the pelage), but some cranial characters are also useful for taxonomic purposes (Table 5).

M. brevicaudata strict sense, *M. touan*, *M.* sp. nov. "touan sul", and *M.* sp. nov. "Trombetas" are readily distinguished from *M. glirina and M. palliolata* by the richer, brighter coloration of the upperparts, commonly gray dorsally and red laterally (versus generally paler coloration, i.e. lighter gray dorsally, and orange laterally) (Figure 4); the color of the ventral fur, which is somewhat cream colored and sharply differentiated from the reddish sides (versus yellowish to orange colored, not sharply differentiated from the orange sides) (Figure 5); the extension of body fur onto the tail, which is longer dorsally than ventrally (versus equally extended on dorsal and ventral sides). Additionally, *M. brevicaudata*, *M. touan*, and *M.* sp. nov "Trombetas" are also distinguished from *M. glirina* and *M. palliolata* by the narrower cap of grizzled-grayish fur confined middorsally by a band of red hairs above each eye, in contrast to the broad cap of grizzled-grayish fur extending over the entire crown of the head, across the eyes in the latter two species.

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Despite the similarity of *M. glirina* and *M. palliolata* on general coloration and pelage patterns, these species can be separated by external and cranial features. When comparing specimens of the same sex and age class, *M. glirina* is larger than *M. palliolata* in most cranial and external dimensions (Table 2). *M. glirina* also differs from *M. palliolata* by its paler lateral fur and middorsal stripe (Figure 4). Some brighter specimens of *M. glirina* and paler specimens of *M. palliolata* are highly similar in dorsal view, but the ventral fur is grayish cream to light orange in *M. glirina*, in contrast to more intense orange in *M. palliolata* (Figure 5). Additionally, the body fur that covers the proximal part of the tail is slightly shorter (commonly one-sixth versus one-fifth of caudal length) and paler in *M. glirina* than in *M. palliolata*. Cranially, despite the smaller size of the skull, *M. palliolata* exhibits broader interorbital region than *M. glirina* (Table 2, Figure 6). Males of *M. palliolata* (and females to a lesser degree) have more developed temporal lines, which converge to form a V-shaped line on the interorbital region of old adult specimens. The zygomatic arches are more convergent anteriorly in *M. palliolata* than in *M. glirina*, giving a more triangular shape to the skull in dorsal view. Generally, the nuchal crests are more developed in *M. glirina*. The palate is proportionally larger in *M. palliolata* than in *M. glirina*, at least across first and second upper molars (Figure 7). Adult males (but apparently not females) of *M. palliolata* have taller upper canines (Table 2).

M. glirina and *M. palliolata* were historically considered synonyms of *M. brevicaudata*. Voss *et al.*, 2001 appropriately recognized them as valid species, providing some external diagnostic characteristics. In this study, we noted some cranial features which are also helpful in distinguishing *M. glirina* and *M. palliolata* from *M. brevicaudata* (as defined here), and strengthen their status of valid species. When comparing specimens of the same sex and age class, *M. brevicaudata* is larger than *M. palliolata*, both externally and cranially (Table 2, Figure 4, 6). The zygomatic arches are slightly more convergent anteriorly in *M. palliolata*, giving a more triangular shape to the skull in dorsal view (Figure 6). In addition, in this species the postorbital constriction is proportionally broader, the maxillopalatine fenestra (Figure 7) and the canine are proportionally longer (Table 2). *M. glirina* and *M. brevicaudata*`s skull are similar in general size, but *M. glirina* shows cranial crests (mainly the nuchal ones) more developed (Figure 6), the zygomatic arches slightly more rounded (mainly anteriorly), larger molars (Table 2), and the maxillopalatine fenestra longer (Figure 7).

M. brevicaudata shares a rich colored pelage with *M. touan*, *M.* sp. nov. "touan sul", and *M.* sp. nov. "Trombetas", as well as a ventral fur sharply differentiated from the reddish sides, and body fur onto the tail more extended on dorsally than ventrally. However, it differs from them

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by the notably less distinct (versus sharply distinct), grayish, brownish or reddish (versus grayish or blackish) midddorsal stripe, which is poorly or non grizzled (versus markedly grizzled) (Figure 4). The grizzled aspect is the resultant contrast between the dark basal band and light distal band of middorsum hairs; as the distal band is yellowish (reddish in some cases) in *M. brevicaudata* and whitish in the other three species, the grizzled aspect is more evident in the latter. *M. brevicaudata* also differs from *M. touan* and *M.* sp. nov. "Trombetas" by the proportionally shorter light tips of ventral hairs, which gives a more grayish aspect to the venter (Figure 5); the general shorter extension of body fur on the dorsal surface of the tail (up to about one fourth versus one third or more of caudal length). Additionally, on the plantar surface of *M. brevicaudata* feet, the thenar pad is subequal to the interdigital pads in general proportions, whereas the thenar pad is clearly longer than the interdigital pads in all other three taxa. However, this characteristic must be considered with caution, as only three specimens of *M. brevicaudata* were analyzed regarding the plantar surface (USNM 490232, 490235, 490247).

M. sp. nov. "touan sul" is readly distinguished from *M. brevicaudata*, *M. touan* and *M.* sp. nov "Trombetas" by the broader (shared with *M. glirina* and *M. palliolata*) and darker cap of grizzled-blackish fur on head (Figure 4). This species show the middorsal stripe noticeably darker (commonly blackish colored versus grayish or brownish colored in the other three species), with sharper distinction from the laterals which exhibit the richest red color in this species. Compared with *M. touan* and *M.* sp. nov "Trombetas", *M.* sp. nov. "touan sul" also shows a less extensive coverage of the tail with body fur (about one fifth versus one third or more of caudal length); the ventral fur slightly more washed with gray; and the feet, tail and ears darker (Figure 9).

M. sp. nov "Trombetas" is highly similar to *M. touan*, but can be distinguished from the latter by the middorsal stripe slightly lighter and less marked; the red lateral fur slightly paler; and the stripe at the crown lighter and more ill-defined (Figure 4). When considered together, these features are reliable for identification purposes, but not consistently efficient due to the great intraspecific variation observed in both species (see the Geographic variation topic).

Cranially, *M. brevicaudata*, *M. touan*, *M.* sp. nov. "touan sul", and *M.* sp. nov. "Trombetas" are highly similar, but *M.* sp. nov. "touan sul" exhibits molars slightly larger (Table 2). No consistent differences were found between *M. brevicaudata*, *M. touan* and *M.* sp. nov. "Trombetas". In average, *M. brevicaudata* is both externally and cranially larger than *M.* sp. nov. "Trombetas" (Table 2), but all dimensions have great overlap and are not useful for

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taxonomic purposes. Although specimens of *M.* sp. nov. "Trombetas" do not differs from *M. touan*, we noticed that when comparing subadult and early adult specimens, males and females of *M. touan* have larger skulls. For example, CBL ranges from 32.55 mm to 33.97mm in females, and 33.75 mm to 35.57 mm in males of age class 5 of *M.* sp. nov. "Trombetas", while CBL ranges from 33.58 mm to 36.86 mm in corresponding females, and from 36.96 mm to 38.08 mm in corresponding males of *M. touan*.

To compare statistically *M. brevicaudata*, *M. touan*, *M.* sp. nov. "touan sul", *M.* sp. nov. "Trombetas", *M. glirina*, *and M. palliolata*, we used a size-free discriminant function analysis (DA), for which we applied the stepwise method. Because differences between sexes and among different adult age classes are mainly releated to size, as we previously showed through univariate statistics analyses, we used all adult age classes and both sexes in DA.

This multivariate test revealed significant differences between *M. glirina* and *M. palliolata*, but not among *M. brevicaudata*, *M. touan* and *M.* sp. nov. "Trombetas" (Figure 10). DA also provided significant separation between *M.* sp. nov "touan sul" and *M. brevicaudata*; *M.* sp. nov "touan sul" and *M. glirina*; and *M.* sp. nov "touan sul" and *M. palliolata*. Additionally, DA partially discriminated *M.* sp. nov "touan sul" *and M.* sp. nov. "Trombetas"; and *M.* sp. nov "touan sul" *and M. touan* (Wilks' lambda = 0.093, F= 12.830, df= 1,696; p=0,000). The canonical loadings indicated that 17 variables had greatest relative contribution to group dispersion, from which the ones with the greatest F- values were UMS, BBC, NB, HC, ZB, BFO, BRO, BIF. The jackknifed classification matrix correctly classified 41% of *M. brevicaudata*, 33% of *M. touan*, 65% of *M.* sp. nov "touan sul", 60% of *M.* sp. nov. "Trombetas", 94% of *M. glirina*, and 85% of *M. palliolata*.

Monodelphis domestica versus *M. glirina*

M. domestica, which has never been recognized as a member of the *brevicaudata* complex before, differs from the remaining species of the complex by the relative larger size and by the dorsal fur entirely gray, without orange or reddish flanks. Due the external similarities between specimens of *M. glirina* from east of the Xingu river, including the holotype of *M. maraxina* (which exhibit upperparts grayish) and *M. domestica*, and the genetic similarity of specimens of *M. domestica* with specimens of the *M. brevicaudata* complex, we provide external and cranial comparisons between these two forms.

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Externally, *M. domestica* has smaller, narrower, and more whitish feet, with paler dorsal scales covered with white (versus cream or grayish) hairs. Caudal scales are also lighter in *M. domestica*, mainly ventrally, and caudal hairs are more visible without magnification, giving to the tail a hairy aspect. In *M. domestica*, the middorsum is gray and the laterals are also gray or tend yellowish, while in *M. glirina* the general coloration is darker, with middorsum gray or dark gray and the laterals tending to orange. In *domestica*, there is a yellowish circumocular area which contrasts with the blackish eyelids. In *M. glirina*, the circumocular area is grayish and does not contrast with the eyelids. Additionally, we found seven mammae in *M. domestica* (specimens LZUFPI 158, MPEG 34994), but nine in *M. glirina* (specimens MPEG 1318, 10134, 38985).

Cranially, *M. domestica* is generally larger; the interorbital region is narrower and more pronounced, which is readily seen in dorsal view; the rostrum is, proportionally, slightly shorter; the maxillopalatine fenestra are broader; the posterolateral palatal foramen is larger, and the posterolateral palatal region is slightly more expanded backward.

Additional species of the *Monodelphis brevicaudata* complex

*Monodelphis "*species A"

We analysed six specimens from Estación Biologica de los Llanos, Guarico, Venezuela that we associated to *Monodelphis* species A of Pine & Handley, 2007 (Figure 1) or *M. orinoci* of Ventura *et al.*, 1998 (see Introduction). Our sample includes four skins (three young specimens and one adult female), one adult male in fluid, and two juvenile skulls (one male and one female).

These specimens exhibit fur color clearly paler than *M. palliolata* and *M. brevicaudata*. The adult female (USNM 443774) is smaller than adult females of *M. palliolata* and *M. brevicaudata*, and has fur clearly shorter and less dense. The middorsal stripe is too light, and as in *M. palliolata* and *M. glirina*, occupies the entire crown of the head between the eyes. The dorsum is light gray, and the laterals are faded orange. The adult male (USNM 490240), in fluid, has the pelage longer than the female and the juveniles from Guarico. The laterals on this specimen are yellow, and the middorsal stripe is dark buff to light brown, instead of grayish, possibly because of some fading effect of the alcohol on the pelage color. Like in the adult female, the middorsal stripe occupies the entire crown of the head between the eyes, and is much lighter than in *M. glirina* and in *M. palliolata*. In the adult male and female, the

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underparts are much lighter than in other species, cream colored (mainly self-colored). In the male, the tail is covered with body fur in a longer extension than in the female, corresponding to less than one third of caudal length. In the male specimen, the skin of the scrotum is gray colored, covered with cream colored hairs; the ears have a general buff coloration, with the tips light brown, and are covered with whitish hairs; the vibrissae are orange; the tail scales are dark buff to light brown, and the short hairs associated to them are yellowish. The ears of the adult male (fluid specimen), when compared with specimens of *M. brevicaudata* (USNM 490232, 490235, 490247) and *M. palliolata* (USNM 448751, 490238), show the antihelix notably less developed, almost indistinct, while in *M. brevicaudata* and mainly in *M. palliolata* it is clearly more developed. Comparisons of the skulls of the two young specimens (USNM 443780, 443776) with those of *M. palliolata* with corresponding sex and age (USNM 517250, 385003) showed that *M. "species A"* has a smaller skull, with smaller upper incisives and tooth row. Plus, the rostrum seems slightly shorter and broader.

Compared with the adult male specimen from Guarico, the type of *Monodelphis orinoci* Thomas, 1899 (BM 98.12.1.22), an early adult male specimen from Caicara, south and east of the Orinoco river, which we include as a representative of *M. brevicaudata*, shows important differences, such as the middorsal stripe darker, grizzled gray instead of buff to light brown, the laterals much more ferruginous instead of yellowish, and the ventral hairs with gray base much more evident.

Therefore, our results support that *M. "species A"* is a validly species, which is morphologically distinct from other species distributed in adjacent areas, namely *M. palliolata* and *M. brevicaudata*, and that the name *M. orinoci* Thomas is not applicable to it. As our sample is too limited in terms of number of adult specimens and skulls, we are not able to provide a formal description of this species at the present time.

Some authors considered that the geographic distribution of *M. orinoci* (actually *Monodelphis "species A"*) extends to the south and east of Rio Orinoco (e. g. Linares, 1998; Pérez-Hernández *et al.*, 1994; Ventura *et al.*, 1998). Linares, 1998 stated that specimens regarded as *orinoci* from the south of Rio Orinoco are darker and slightly larger than the ones from the north, which have previously been referred as *Peramys brevicaudatus dorsalis* Allen, 1904. We analysed the type series of *dorsalis* and agree with Voss *et al.*, 2001 that it represents *M. brevicaudata*. As well, all specimens from the south and east of Rio Orinoco analyzed by us were assigned to *M. brevicaudata*. For that reasons, we believe that *Monodelphis "species A"* are restricted to the opposite side of Rio Orinoco.

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Specimen from Manaus, Amazonas

The single specimen of Manaus from which the cyt b sequence was available was examined by us through photographs. According to the external measurements and the large head size relative to the body, it appears to be a very young specimen. Morphologically, the specimen does not have the middorsal fur distinct from the laterals, showing upper fur homogeneously reddish; has a short extension of body fur onto the tail; and the ventral fur is much reddish, being not differentiated from the laterals. According to our morphological analyses of *M. brevicaudata*, *M. palliolata*, *M. glirina*, *M.* sp. nov. "Trombetas", *M. touan*, and *M.* sp. nov. "touan sul", for which we had samples of very young specimens, juveniles do not have the external features of coloration and body fur extension onto the tail well defined (see also the non geographic variation topic above). This must be the case for the specimen from Manaus, which represents a distinct species on the basis of our molecular analyses.

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DISCUSSION

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Species diversity

Our data provide strong support for three defined clades within the assemblage of forms recognized by Voss *et al.*, 2001 as an unnamed form (*M.* species D from Pine & Handley, 2007), and under the name *M. brevicaudata*, in which we recognized four distinct species. The northwestern clade, composed of specimens from north Guyana and Venezuela, retains the name *M. brevicaudata* Erxleben, 1777. The central clade, containing specimens from south of Guyana and west of the Brazilian state of Pará, is associated with a new form, described here as *Monodelphis* sp. nov. "Trombetas". The east clade consists of samples representing two morphologically distinct taxa - one with specimens from French Guyana and the Brazilian state of Amapá, for which the name *Viverra touan* Shaw, 1800 is available, and the other with specimens from eastern Pará, precisely from south of the Amazon river and east of the Xingu river, also recognized herein as a distinct species, described as *Monodelphis* sp. nov. "touan sul".

Since specimens from the east clade, precisely from north of the Amazon river, did not clustered as a monophyletic group (see Figure 2), we could have been conservative and keep the name *touan* restricted to specimens from Cayenne, French Guiana (the nominal taxon type locality). Conversely, we preferred to extend the name *touan* to all specimens from north of the Amazon river, since they comprise a group readily diagnosable and distinct in terms of

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external morphology from specimens of *M.* sp. nov. "touan sul". Therefore, even in the absence of resolution in our molecular analyses, we accepted morphological evidence for recognizing *M. touan* as a valid species (see further discussion about the phylogenetic relationships inside *M. touan*).

Additionally to the four species mentioned above, we found a fourth divergent lineage represented by a single specimen from Conjunto Parque do Roxinol, Manaus (INPA 2854). We were not able to provide diagnostic morphologic features for this lineage, because the voucher is an immature specimen in fluid, which we analyzed through photographs. Despite that, our results lead us to think this might represent a distinct species, for which we are not aware of any available names. The few adult specimens from Manaus and Itacoatiara included in this study as *M.* sp. nov. "Trombetas" have no tissue samples. Interestingly, they show some morphological features that distinguish them from the remaining specimens of *M.* sp. nov. "Trombetas" (see above the topic Geographic variation of the species *M.* sp. nov. "Trombetas"). Although these features could suggest that the adult specimens from Manaus and Itacoatiara are representatives of the fourth lineage of our molecular analyses, we could not associate them with the single immature specimen from Manaus for which we have cyt b sequences. Additionally, since the intraspecific variation within *M.* sp. nov. "Trombetas" appears to be great (see the topic Geographical Variation of this species) and not completely understood, we see no reasons at the present time to consider the specimens from Manaus and Itacoatiara as a distinct species. Further morphological and molecular analyses of adult specimens from Manaus are necessary to determine the diagnostic characters and geographic distribution of the species represented by the fourth lineage of the present report.

In spite of the high intern mean divergence (4.4% to cytb; Table 1) and high variability found in the morphologic analysis, molecular sub groups within *Monodelphis glirina* were highly variable, generally with low support values, resulting in a basal politomy in most consensus trees. Therefore, even with our results suggesting that this species may correspond to a complex of species, at this point we could not determine with certainty any consistent divisions.

M. maraxina holotype show the external and cranial morphology highly similar whit specimens of *M. glirina* from east of the Xingu river, and therefore, *M. maraxina* is actually a synonym of *M. glirina*.

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Specimens of *M. domestica* grouped with the *M. brevicaudata* complex in our analyses. Studies of Patton & Costa, 2003 had previously indicated phylogenetic affinities between *M. domestica* and *M. brevicaudata*, and Pine & Handley, 2007 suggested that *M. domestica* and *M. brevicaudata* are sister groups. Our results confirm a strong phylogenetic proximity of these forms. As mentioned before, representatives of *M. domestica* included in this study composed two divergent clades geographically structured and with considerable genetic distance, suggesting that at least two species may be concealed under this name - one composed of specimens from northeastern Brazil and another comprising specimens from west central Brazil. However, the biogeographical interpretation of these results and the taxonomic revision of *M. domestica* are beyond the scope of this study.

We agree with Voss *et al.*, 2001 in recognizing *M. palliolata* as a valid species. Lew *et al.*, 2005 studied the relationship between skull size and shape in species of *Monodelphis* from Venezuela using multivariate analyses, and their results also support the recognition of *M. palliolata* as a distinct species.

Specimens assigned to the *Monodelphis* species A of Pine & Handley, 2007 represents a distinct and unnamed species according with our results, which we were not able to study thoroughly and provide a formal description due to limited sample size. Many authors previously referred to this form as *M. orinoci*, some of which already indicated external, cranial, and ecological differences between them and other *Monodelphis* species (e.g. Lew *et al.*, 2005; Linares, 1998; Pérez-Hernández *et al.*, 1994; Ventura *et al.*, 1998), but any one analyzed the type specimen of *M. orinoci* (Thomas, 1899) to confirm this application. Our results indicate that the savanna specimens, which are represented in our sample by specimens from Estacion Biologica de los Llanos, do not correspond to the type specimen of *M. orinoci* Thomas (which we include as a representative of *M. brevicaudata*), and therefore merits a new name.

In summary, we formally recognize nine species in the *Monodelphis brevicaudata* complex: *M. brevicaudata, M. touan, M. glirina, M. palliolata, M. domestica*, *M.* sp. nov. "touan sul", *M.* sp. nov. "Trombetas", *M.* "species A", and *M.* sp. "Manaus". Some of the recognized forms (*M. glirina* and *M. domestica*) may actually represent species complexes.

Since we use only molecular sequences in the phylogenetic analyses, we associated the specimens to a name according to the morphology of voucher specimens within the monophyletic clades (see discussion below for the only exception, *M. touan*). Although

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external morphology showed to be useful for diagnosing all species, intraspecific variation showed to be great and not completely known. Therefore, identifying specimens based solely on morphology may be difficult sometimes, and the inclusion of molecular samples to help this task is recommended.

Phylogenetic relationships within *M. touan*

With the absence of resolution in molecular analyses for the phylogenetic relationships of specimens of *M. touan*, some scenarios could be possible to explain the results obtained in this study. First, the *M. touan* haplotypes could form a monophyletic group although this relationship was not recovered here, due to weak phylogenetic signal, for example. According to Funk & Omland, 2003, although rapidly evolving mitochondrial sequences are less prone to inadequate information than most loci, even mtDNA may exhibit insufficient variation for the accurate reconstruction of very recent phylogenetic radiations. Consequently, even if the studied species are in fact monophyletic, a reconstructed gene tree may erroneously do not exhibit this history. Wiens & Penkrot, 2002 predict that species will generally become exclusive in their mtDNA haplotype phylogenies long before becoming exclusive in morphology-based phylogenies and before acquiring diagnostic morphological characters. Following this assumption, since *M. touan* and *M.* sp. nov. "touan sul" are morphologically diagnosable and different from each other, the monophyly of *Monodelphis touan* could be the real scenario, and probable had not been recovered here because of inadequate phylogenetic information.

Alternatively, the haplotypes of the east clade from the north of the Amazon river could actually represent more than one species. However, since there is no morphological evidence that support this hypothesis, and considering the relative low intraspecific genetic divergence among the subgroups formed, we think this does not appear to be the case.

As a third hypothesis, specimens of *M. touan* could have a nonexclusive gene (cyt b/ 16 s) genealogy, composing a paraphyletic group. Given enough time, distinct species will have exclusive DNA haplotype phylogenies relative to other species (Neigel & Avise, 1986), i.e. they will be monophyletic. However, as exposed by some authors (e. g. Funk & Omland, 2003; Neigel & Avise, 1986), because of incomplete lineage sorting of ancestral polymorphisms species may be nonexclusive at some point in their history. According to these authors, incomplete sorting of ancestrally polymorphic allelic lineages can have especially major effects in the case of rapidly radiating taxa. For the species that have diverged very recently, the individuals or populations can be paraphyletic or polyphyletic with respect to one or more

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other species. Therefore, species may be distinct and even morphologically diagnosable from each other but still have nonexclusive gene genealogies (Wiens & Penkrot, 2002). According to Wiens & Penkrot, 2002, this scenario may be common when a species with a large geographic range and a large population size gives rise to a diagnosable distinct species with a much smaller range (i.e. a peripheral isolate), such that the latter species quickly becomes exclusive, whereas the former species does not. This scenario appears to be the most applicable to *M. touan.*

The origin of *Monodelphis* sp. nov. "touan sul"

If the haplotypes of *M. touan* compose a monophyletic or paraphyletic assemblage we cannot conclude at this point. However, regardless the real phylogenetic relationships of these haplotypes, we are able to propose that *M.* sp. nov. "touan sul" originated from *M. touan*, probably through a recent peripheral isolation and subsequent speciation of some southern populations.

M. touan has higher intraspecific genetic divergence (mean 1.2%) when compared to specimens of *M.* sp. nov. "touan sul" (mean 0.7%). The divergence between *M.* sp. nov. "touan sul" and *M. touan* is larger (mean 2.6%), but still small when compared to other interspecific divergence values in the *brevicaudata* complex (mean 6.5% between *M. touan* and *M.* sp. nov. "Trombetas", the lowest divergence value among the remaining species of the complex). Considering a similar rate of evolution for both species, these results suggest that *M. touan* had more time to accumulate mutations and, consequently, to increase its intraspecific genetic divergence. On the other hand, *M.* sp. nov. "touan sul" seems to have arisen recently, given its reduced genetic variability. Taking into account the mentioned divergence values and the topologies obtained in our phylogenetic analyses, which always recovered a monophyletic *M.* sp. nov. "touan sul" clade within a clade of *M. touan* haplotypes, we conclude that *M. touan* gave rise to the *M.* sp. nov. "touan sul" lineage.

Steiner & Catzeflis, 2004, studing the genetic variation and geographic structure in *Monodelphis brevicaudata* (sensu Voss *et al.*, 2001), included specimens recognized here as *M. touan*, *M.* sp. nov. "touan sul", *M. brevicaudata*, and *M.* sp. nov. "Trombetas" in their analysis of cyt b sequences. The authors showed that the ancestral haplotypes come from French Guiana (*M. touan*), followed by Guyanan and Venezuelan haplotypes (*M.* sp. nov. "Trombetas", *M. brevicaudata*). This result also suggests that *M. touan* had an anterior origin to *M.* sp. nov. "touan sul".

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The low genetic divergence between *M.* sp. nov. "touan sul" and *M. touan* could be explained by the recent separation of these species. Additionally, a recent origin of *M.* sp. nov. "touan sul" seems highly probable given the low internal genetic difference showed by its members. Because a short period of time has passed since the appearance of *M.* sp. nov. "touan sul", there are few autapomorphies for each species. This could explain the difficulty to recover the monophyly of the ancestral species (in a case of monophyly of *M. touan*), as well as a nonexclusive gene genealogy (in a case of pharaphyly of *M. touan*).

Hull *et al.*, 2008 provided a practical example of speciation of peripheral population isolation, showing a case where an island archipelago hawk – *Buteo galapagoensis* – rise up from a mainland and widespread taxon – *Buteo swainsoni*, rendering *B. swainsoni* paraphiletic with respect to *B. galapagoensis*. Hull *et al.*, 2008 found low estimates of divergence on mitochondrial control region (mean 1.79%) between *B. galapagoensis* and *B. swainsoni*, a smaller divergence among haplotypes of *B. galapagoensis* (mean 0.54%) and a proportionally larger divergence (mean 1.68%) among *B. swainsoni* haplotypes. These genetic distances are in agreement with those found by us in *M.* sp. nov. "touan sul" and *M. touan*, but in the *M. touan* case, the Amazon river instead of the sea may act as a barrier, and *M.* sp. nov. "touan sul" fits as the island daughter species.

It is known that these set of populations named here as *M.* sp. nov. "touan sul" and *M. touan* are geographically isolated by the Amazon river and, consequently, are not able to exchange genes. So, it seems that the achievement of the reciprocal monophyly between these lineages, if not reached yet, is a question of time.

Morphology and genetics: convergence and divergence

Even though external morphology showed to be useful for diagnosing the genetic distinct groups, some discordance was observed. Generally, despite the high genetic divergence among the species dismembered from *M. brevicaudata* sensu Voss *et al.*, 2001, we found only medium to little divergence in external morphology, and little to no divergence in skull morfology.

Discriminant Analysis of cranial measurements were not meaningful in detecting species structure among the mentioned species, being useful only to separate *M.* sp. nov. "touan sul" from *M. brevicaudata*, *M. glirina* and *M. palliolata*, and to separate *M. glirina* from all other species tested (Figure 10). DA showed overlapping values in the first two axes for *M.*

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brevicaudata, *M.* sp. nov. "Trombetas", *M. touan*, and *M.* sp. nov. "touan sul", suggesting that within-group variability largely exceeds between group variability, and that these species have a similar skull, as noted in our direct analyses of skull morphology.

We conclude that the degree of genetic divergence is not necessarily followed by a proportional degree of morphological differentiation within the group. This is evident when we note that *M.* sp. nov. "touan sul" is readily morphologically distinguished from *M. touan* despite the relatively small genetic divergence (average 2.6%), while *M. touan* and *M.* sp. nov. "Trombetas" are weakly differentiated in morphology even showing a high value of genetic distance (average 6.5%).

Alternative explanations may be invoked to explain this controversial pattern of low morphological divergence between high genetic divergent species and high morphological divergence between low genetic divergent species. Considering the high genetic distance between *M.* sp. nov. "Trombetas" and *M. touan*, phylogenetic signals from morphological characters may be obscured by homoplastic evolution in these species, that evolved in similar ecosystems and selective pressures, but on physically separated areas (considering alopatric distribution to the species in question). This could be applicable also to *M. brevicaudata*, but this species is more easily morphologically discriminated from *M.* sp. nov. "Trombetas" and *M. touan* than these latter are from each other.

On the other hand, the clear morphological differences between *M.* sp. nov. "touan sul" and *M. touan* appear to be explained by a rapid morphological evolution of *M.* sp. nov. "touan sul". Rapid phenotypic changes of isolated populations from an ancestral phenotype have been reported for other species of mammal and birds (e. g. Hull *et al.*, 2008; Maldonado, Hertel & Vila, 2004; Rasner *et al.*, 2004; Talbot & Shields, 1996). Several processes have been cited as causes for this rapid phenotypic change, including founder event, change in selective landscape, relaxation of interspecific competition, and niche expansion (Grant, 1998; Hull *et al.*, 2008; Rasner *et al.*, 2004; Talbot & Shields, 1996; Whittaker, 1998). Differences in the habitat or interspecific competition seem not to be the main processes involved in the evolutionary history of *M.* sp. nov. "touan sul" and *M. touan*. Nevertheless, as allopatric species separated by the Amazon river, genetic drift appears to have a greater contribution for the observed morphological differences between these species. As in molecular markers, morphology may change more rapidly in small populations due to stochastic sampling (Hull *et al.*, 2008). Given a "parental" species (*M. touan*) with geographic substructure and a small peripheric speciating population (*M.* sp. nov. "touan sul"), it is expected that this population

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will initially possess a phylogenetically restricted subset of parental alleles and may lose alleles under drift at a faster rate than the larger parental population (Funk & Omland, 2003).

Species Distribution – the role of rivers in generating and maintaining diversity in the *M. brevicaudata* complex

M. brevicaudata, *M. touan*, *M.* sp nov. "touan sul", and *M.* sp. nov. "Trombetas" exhibit closer phylogenetic relationship among each other than they do with *M. glirina* and *M. domestica* (Figure 2). This phylogeographical pattern suggests at least two diversification centers for the complex, one on the Guiana shield, comprising species distributed mainly on north of the Amazon river (plus *M.* sp nov. "touan sul", which is distributed on south of this river), and other on Brazilian shield, comprising *M. glirina* and *M. domestica*.

Additionally, *M.* sp. nov. "Trombetas" place as basal to *M. brevicaudata*, *M. touan* and *M.* sp nov. "touan sul" in most phylogenetic analyses, but the relationship among the last three, as well as between *M. domestica* and *M. glirina*, were not recovered in this work. The difficulties in determining the evolutionary relationships of these species may be related to the existence of sequential rapid radiation events in this group, and higher molecular efforts are needed to investigate this question.

Rivers have been suggested to have played an important role in shaping present-day patterns of ecological and genetic variation, as well as species distribution among Amazonian species and communities in several distinct taxa (e.g. Aleixo, 2004; Ayres & Clutton-Brock, 1992; Capparella, 1988; Cheviron, Hackett & Capparella, 2005; Funk *et al.*, 2007; Hershkovitz, 1977; Lehmam, 2004; Moritz, Schneider & Wake, 1992; Peres, Patton & da Silva, 1997; Resmen Jr & Parker III, 1983; Roosmalen, Roosmalen & Mittermeier, 2002; Torres-Pérez *et al.*, 2007).

Along the distribution of the *Monodelphis brevicaudata* complex, major rivers seem to have participated in genetic differentiation and phylogeographic structure of the species. Certainly for some species and apparently for other, the rivers limit or greatly reduce the gene flow between opposite margins, being responsible for at least the maintenance of diversity, and for defining the geographic boundaries of species.

Rivers that were found as effective geographic barriers for the species herein studied are the Amazon river, which is the northern limit for *M. glirina* and *M.* sp. nov. "touan sul", and the southern limit for *M.* sp. nov. "Trombetas" and *M. touan*; the Xingu river, which is the western

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limit for *M.* sp. nov. "touan sul", and a possible barrier for phenotypically divergent populations of *M. glirina*; the Orinoco river, which is the northern limit for *M. brevicaudata*. Additionally, the Tocantins river appears to be the western limit for *M. domestica*, and the eastern limit for *M. glirina*. However, habitat requirements may also limit the geographic distributions of these species, as *M. glirina* has been associated to forested areas in the Amazon biome, and *M. domestica* to open vegetation areas in the Cerrado biome. There are no records for species of the *M. brevicaudata* complex at the western margin of the Negro river, suggesting that this river also acts as a geographic barrier for this group.

The geographic frontiers between *M.* sp. nov. "Trombetas" and *M. touan*, and between the former and *M. brevicaudata* are not known, but following the allopatric distribution patterns generally observed for the group (except for *M.* sp. nov. "touan sul" and *M. glirina*, which are sympatric in some localities on south of the Amazon river and east of the Xingu river), no simpatry is expected. *M.* sp. nov. "Trombetas"and *M. brevicaudata* were found to be adjacently distributed in Guyana, with the former occurring in the center and south of this country, and the latter in the north. Among the rivers that cross these areas are the Potaro river, which was reported by Lehmam, 2004 as a river that prevent the dispersal of monkeys in Guyana, and could also separates the mentioned species of *Monodelphis.* An alternative barrier for these species could be the savanna formations associated to the Pakaraima Mountains lying in the western Guyana, although we were not able to empirically test it based on our samples at hand. Our geographic samples of *M.* sp. nov. "Trombetas" and *M. touan* are too scarce to suggest any putative frontier between them.

Riverine barriers will result in allopatric divergence, as they involve vicariant processes (Patton & da Silva, 1998). Therefore our results let us to think that vicariance – rather than dispersal events – seem to be responsible for the present genetic and phylogeographic patterns observed along the range of the brevicaudata group, which include the Guiana and Brazilian shields.

According to Patton & da Silva, 1998, a general model of riverine diversification predicts that (1) populations on one side will be monophyletic relative to those on the opposite side, and (2) that the sets of opposite-bank populations will form a sister group relative to those from elsewhere in the species range. At this point, we could not recover if these assumptions are true for the studied group, but certainly most of the taxa investigated through molecular data are monophyletic. Although we lack data to confirm the models of speciation in the *M.*

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brevicaudata complex, we posit the hypothesis of riverine diversification to be tested in future studies.

The vicariant assumption is less likely to be hypothesized for *M.* sp. nov. "touan sul", which had a more recent origin probably through a peripheral isolation and subsequent speciation of some southern populations of *M. touan*. Since the origin of this species appears to be much more recent than the others, (see the topic about the origin of *M.* sp. nov. "touan sul" above), it is also possible that a dispersal event of some southern populations of *M. touan* through the Amazon river have occurred.

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APPENDIX A

List of specimens employed in the phylogenetic analysis. The appendix uses updated taxonomy. New sequences obtained in this work are indicated by a "X" replacing the GenBank Accession No, which will be available as soon as Pavan et *al.* is submitted. Sequences obtained through the courtesy of Dr. James L. Patton (MVZ, Berkley) are indicated by a superscript "JLP" following the Voucher Number, and that ones obtained from Gen Bank are indicated by an asterisk next to the GenBank Accession No. Voucher numbers in bold face refer to specimens for which we did not perform morphological analyses. Uncatalogued specimens are referred by collector number: Ana P. Carmignotto (APC), Bárbara A. Costa (BAC), Leonora P. Costa (LPC), Louise H. Emmons (LHE), Miguel T. Rodrigues (MRT), Omar Linares (L). Specimens with the initials CAX, CGC, CN, CT, JUR, MAR, and PSA will be deposited in the MPEG collection. Specimens with the initials IT-M, StoAn, and UUPI will be deposited in the MZUSP collection.

Species	Voucher Number (museum or collector)	Locality Data	GenBank Accession No.	
			Cyt-*b*	16S rDNA
M. brevicaudata	L-1917	Rio Caroni, Bolívar, Venezuela	AJ606460*	x
M. brevicaudata	L-1918	Rio Caroni, Bolívar, Venezuela	AJ606459*	x
M. brevicaudata	L-1920	Rio Caroni, Bolívar, Venezuela	AJ606458*	x
M. brevicaudata	ROM 98909	Waikerebi, Barima-Waini, Guyana	AJ606461*	
M. brevicaudata	USNM 568009	Baramita, Barima-Waini, Guyana	AJ606457*	
M. touan	ISEM V-937	Macouria, French Guiana	AJ606455*	
M. touan	ISEM V-1125	Saul, French Guiana	AJ606456*	x
M. touan	ISEM V-1563	Cayenne, French Guiana		x
M. touan	ISEM V-1568	Cayenne, French Guiana	x	x
M. touan	**ISEM V-1574**	Cayenne, French Guiana	x	x
M. touan	**ISEM V-1753**	Awala-Yalimapo, French Guiana	x	x
M. touan	**ISEM V-1752**	Awala-Yalimapo, French Guiana	x	x
M. touan	IEPA 165	Ferreira Gomes, Amapá, Brazil	x	x
M. touan	IEPA 173	Ferreira Gomes, Amapá, Brazil	x	x
M. touan	IEPA 307	Vitória do Jari, Amapá, Brazil	x	x
M. touan	IEPA 909	Pedra Branca do Amapari, Amapá, Brazil	x	x
M. touan	IEPA 913	Pedra Branca do Amapari, Amapá, Brazil	x	x
M. touan	IEPA 1155	Vitória do Jari, Amapá, Brazil	x	x
M. touan	IEPA 1166	Laranjal do Jari, Amapá, Brazil	x	x
M. touan	**IEPA 1375**	Laranjal do Jari, Amapá, Brazil	x	x
M. sp. nov. "Trombetas"	ROM 108477	Potaro-Siparuni, Guyana	AJ606462*	
M. sp. nov. "Trombetas"	**BAC 215**	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38052	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38054	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38056	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38063	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38074	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38093	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 38095	Potro Trombetas, Pará, Brazil		x
M. sp. nov. "Trombetas"	MPEG 39810	Potro Trombetas, Pará, Brazil	x	x

Species	Voucher Number (museum or collector)	Locality Data	GenBank Accession No.	
			Cyt-*b*	16S rDNA
M. sp. nov. "Trombetas"	MPEG 39811	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	MPEG 39812	Potro Trombetas, Pará, Brazil	x	x
M. sp. nov. "Trombetas"	CN 52	Faro, Pará, Brazil,	x	x
M. sp. nov. "Trombetas"	CN 166	Alenquer, Pará, Brazil	x	x
M. sp. nov. "touan sul"	**INPA 2834** [JLP]	Marabá, Pará, Brazil		
M. sp. nov. "touan sul"	CAX 593	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 427	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 872	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 880	Portel, Pará, Brazil		x
M. sp. nov. "touan sul"	MAR 919	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 1023	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 1049	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MAR 1151	Portel, Pará, Brazil	x	x
M. sp. nov. "touan sul"	MPEG 39762	Anapú, Pará, Brazil		x
M. sp. nov. "touan sul"	PSA 44	Marabá, Pará, Brazil	x	x
M. sp. nov. "touan sul"	PSA 45	Marabá, Pará, Brazil	x	x
M. sp. nov. "touan sul"	PSA 61	Marabá, Pará, Brazil	x	x
M. sp. nov. "touan sul"	PSA 63	Marabá, Pará, Brazil	x	
M. sp. nov. "touan sul"	PSA 116	Marabá, Pará, Brazil		x
M. sp. nov. "touan sul"	PSA 158	Marabá, Pará, Brazil		x
M. sp. nov. "touan sul"	PSA 169	Marabá, Pará, Brazil	x	x
M. sp. "Manaus"	INPA 2854 [JLP]	Manaus, Amazonas, Brazil		
M. glirina	MN 59606	Juruena, Mato Grosso, Brazil	x	x
M. glirina	APC 161	Juruena, Mato Grosso, Brazil	X	x
M. glirina	MN 59607	Juruena, Mato Grosso, Brazil	x	x
M. glirina	MN 59608	Aripuanã, Mato Grosso, Brazil	x	x
M. glirina	APC 200	Aripuanã, Mato Grosso, Brazil	x	x
M. glirina	APC 221	Aripuanã, Mato Grosso, Brazil		x
M. glirina	APC M968408	Apiacás, Mato Grosso, Brazil		x
M. glirina	**APC M968431**	Apiacás, Mato Grosso, Brazil	x	x
M. glirina	**APC M968434**	Apiacás, Mato Grosso, Brazil	x	x
M. glirina	**APC M968435**	Apiacás, Mato Grosso, Brazil	x	x
M. glirina	**APC M968450**	Apiacás, Mato Grosso, Brazil		x
M. glirina	**LPC 568** [JLP]	Alta Floresta, Mato Grosso, Brazil		
M. glirina	**LHE 870** [JLP]	Centro, Pando, Bolívia		
M. glirina	MPEG 39813	Vitória do Xingu, Pará, Brazil	x	x
M. glirina	MPEG 39780	Vitória do Xingu, Pará, Brazil	x	x
M. glirina	MPEG 39784	Vitória do Xingu, Pará, Brazil		x
M. glirina	CT 12	Jacareacanga, Pará, Brazil	x	x
M. glirina	CT 15	Jacareacanga, Pará, Brazil	x	x
M. glirina	CGC 01	Canaã dos Carajás, Pará, Brazil	x	x
M. glirina	MPEG 38928	Marabá, Pará, Brazil	x	x
M. domestica	**MRT 3845**	Paranã, Tocantins, Brazil		x
M. domestica	**MRT 3886**	Paranã, Tocantins, Brazil	x	x
M. domestica	**APC 818**	Peixe, Tocantins, Brazil	x	x
M. domestica	**APC 852**	Peixe, Tocantins, Brazil	x	x
M. domestica	**APC 601**	Mineiros, Goiás, Brazil	x	x
M. domestica	**APC 702**	Chapada dos Guimarães, Mato Grosso, Brazil	x	x
M. domestica	**APC 836**	Chapada dos Guimarães, Mato Grosso, Brazil		x
M. domestica	**MTR 11224**	Santo Inácio, Bahia, Brazil	x	x
M. domestica	**MRT 133**	Pacoti, Ceará, Brazil		x

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APPENDIX A. Continued..

Species	Voucher Number (museum or collector)	Locality Data	GenBank Accession No.	
			Cyt-*b*	16S rDNA
M. domestica	**MRT 174**	Pacoti, Ceará, Brazil	x	x
M. domestica	**UUPI 168**	Uruçuí-Una, Piauí, Brazil	x	x
M. domestica	**UUPI 402**	Uruçuí-Una, Piauí, Brazil	x	x
M. domestica	LZUFPI 201	Castelo do Piauí, Piaui, Brazil	x	x
M. domestica	LZUFPI 1098	Brasileira, Piaui, Brazil	x	x
M. emiliae	JUR 13	Juruti, Para, Brazil	x	x
M. Kunsi	APC 860	Peixe, Tocantins, Brazil	x	x
M. sorex	IT-M0088	São Bernardo, São Paulo, Brazil	x	x
M. scalops	IT-M0153	São Bernardo, São Paulo, Brazil	x	x
M. inheringi	**StoAn27**	Santo André, São Paulo, Brazil	x	x
Caluromys philander			AJ628362*	AF166345*
Didelphis marsupialis			AJ606420*	DQ283321*

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APPENDIX B

List of specimens examined and collecting localities. Uncatalogued specimens are referred by collector numbers: Ana Paula Carmignotto (APC), Bárbara A. Costa (BAC), Carla G. Bantel (CGB), Omar Linares (L-), Simone L. Freitas (SLF). Specimens with the initials BML, CAX, CGC, CN, CT, IARVD, MAJ, MAR, PSA will be deposited in the MPEG collection.

Monodelphis brevicaudata: BRAZIL – *Amazonas,* Barcelos, Igarapé do Bigorna, Rio Aracá (MN 69058): -0.25, -63.12; Barcelos, Igarapé Japomeri, left bank of Rio Padauiri (MN 69367, 69371): 0 -64; Barreira, right margin of Rio Jufari (CGB 82, 90): -1,05 -62,15 (Only Photos); *Roraima*, Barreira, left margin of Rio Jufari (CGB 80, 81): -1,01 -62,12 (Only Photos). GUYANA – *Barima-Waini*, Baramita, North West Of Airstrip (USNM 568009): 7,37 -60,49; Waikerebi (ROM 98909): 7,53 -59,4 (Only Photos); *Cuyuni-mazaruni*, Kamakusa (AMNH 140465): 5,95 -59,9; Kartabo (AMNH 48133): 6,38 -58,68; *Upper Demerara-Berbice*, Dubulay Ranch (AMNH 268060): 5,68 -57, 87; *Without locality data* (BMNH 67.4.12.540 [holotype of *brevicaudata*], 88.1.31.1 [holotype of *hunteri*]) (Only Photos). VENEZUELA – *Amazonas*, Capibara, Brazo Casiquiare, 106 Km SW Esmeralda (USNM 406907, 406908, 415277): 2,62 -66,32; Esmeralda, 290 Km S, 235 Km E Pto. Ayacucho (USNM 385010): 3,18 -65,55; Raya, 32 Km S Pto. Ayacucho (USNM 406910 – 406913): 5,4 -67,65; Tamatama, Rio Orinoco (USNM 388355, 388357, 406906, 490231 – 490233, 490235): 3,17 -65,82; *Bolívar*, Caicara del Orinoco (BMNH 98.12.1.22 [holotype of *orinoci*]) 7.63 -66.17; Cuidad Bolívar (AMNH 16124, 16125 [paratypes of dorsalis], 16126 [holotype of dorsalis - Only Photos]): 8,13 -63,55; El Manaco, 65 km SSE El Dorado, (USNM 385005): 6,17 -61,35; Rio Caroni, environs village Rio Claro (L-1917, 1918, 1920): 7,92 -63,02 (Only Photos); Rio Supamo, 50 Km SE el Manteco, (USNM 385004): 7 -62,25; San Ignacio De Yuruaní (USNM 448511, 448512, 448750): 5 -61; Santa Lucia De Surukun, 45 Km NE Icabarú (USNM 443781, 443782, 490247): 4,55 -61,42.

Monodelphis touan: BRAZIL – *Amapá*, Callçoene (USNM 543303): 2,5 -50,95; Ferreira Gomes, Floresta Nacional do Amapá, Igarapé do Braço (IEPA 165, 173): 1,30 -51,59; Ferreira Gomes, Rio Araguari, Fazenda Califórnia, 90 km leste Ferreira Gomes (MZUSP 9933): 0,9 -51,5; Laranjal do Jari, Cachoeira Santo Antônio, Rio Jari (IEPA 1166): -0,05 -51,60; Laranjal do Jari, Reserva Extrativista Cajari, Marinho (IEPA 1143, 1156, 1157): -0,59 -52,24; Macapá (MZUSP 9932): 0,03 -51,05; Macapá, Parque Zoobotânico de Macapá (IEPA 19, 1158): 0,83 -52,04; Mazagão, Ig. Rio Branco, Boa Fortuna, Rio Maracá (MPEG 2500, 2515): -0,3 -52,23; Pedra Branca do Amapari, Parque Nacional Montanhas do Tumucumaque, Rio Amapari (IEPA 305): 1,60 -52,49; Pedra Branca do Amapari, Parque Nacional Montanhas do Tumucumaque, Rio Anacui (IEPA 909,

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913): 1,84 -52,74; Porto Grande, Colônia Matapi (MPEG 33907): 0,68 -51,43; Serra do Navio (MN 24547, 24548, 20221 – 20227, MPEG 8682, 8683, 8772, 12929, 15218 – 15224, 15226 – 15229, 20146, 20147, MZUSP 11692, USNM 393423 – 393436, 393438 – 393442, 461433 – 461435): 0,98 -52,05; (USNM 392050, 392051): 2 -52; Terezinha, Rio Amapari (MZUSP 11693, 24151): 0,97 -52,03; Vitória do Jari, Reserva de Desenvolvimento Sustentável do Rio Iratapuru, Rio Cupixi (IEPA 1154, 1155): 0,63 -51,80; Vitória do Jari, Reserva do Desenvolvimento Sustentável do Rio Iratapuru, Rio Jari (IEPA 307): 0,28 -53,11; *Without locality data* (MPEG 15217). **FRENCH GUIANA – *Arataye***, River Arataye, right bank (USNM 578009): 4,03 -52,7; *Cayenne*, (FMNH 21720 [neotype of *touan*] - Only Photos), Montagne du Tigre (ISEM V-1084), Camp du Tigre (ISEM V-1563, 1568): 4,91 -52,29; *Macouria,* Savane (ISEM V-937): 4,92 -52,37; *Paracou*, near Sinnamary (AMNH 267000): 5,28 -52,92; *Saul* (ISEM V- 1125): 3,62 -53,22; *Tamanoir*, Mana River (FMNH 21793): 5,15 -53,75.

*Monodelphis glirina***: BOLIVIA – *Pando***, Santa Rosa (AMNH 262398, 262399): -12,22 -68,4. **BRASIL – *Acre***, Sena Madureira, Bairro do Triângulo (MPEG 10694 – 10697): -9,07 -68,67; Sena Madureira, Rodovia Manoel Urbano, BR-364, km 8 (MPEG 10553, 12738): -8,88 -69,3; *Amazonas*, Humaitá, Escola Agrotécnica, BR 319, Km 8 (MPEG 34395): -7,5 -63,02; Humaita, Br 230, Km 968 (USNM 545553), Km. 969 (USNM 545552), Km 970 (USNM 545554), Km 974 (MPEG 12745): -7,52 -63,03; Humaitá, BR-230, Km 150, Fazenda Vista Alegre, margem direita Rio dos Marmelos (MPEG 22690): -7,96 -61,85; *Mato Grosso*, Apiacás (MN 59609, 59610, APC M968431, M968434, M968435, M968450, M968408): -9,57 -57,39; Aripuanã (APC 200, 202, 221, 222, 225, MN 59608): -10,18 -59,45; Aripuanã (USNM 545555 – 545557, 545570 – 545582), Cidade Laboratório de Humboldt (MPEG 12718 – 12735, 12749, 12934, 12935, 12937 – 12940, 12952, USNM 545558 – 545569): -9,17 -60,63; Juruena (APC 148, 158, 159, 161, MN 59606, 59607,): -10,32 -58,49; *Pará*, Altamira, 18 Km S e 19 Km W, Agrovila da União (MPEG 15284, 15310, USNM 521431, 521508): -3,18 -53,75; Altamira, 19 Km S e 18 Km W, Agrovila da União (MPEG 8934, 8936, 11528 – 11532, 15347, USNM 521509, 521510): -3,37 -52,38; Altamira, 54 Km S e 150 Km W (MPEG 8928 – 8933, 8935, 8937, 8938, 11390, 15400 – 15404, 15465, 24014, USNM 519727, 519728, 521429, 521430, 521501 – 521507): -3,68 -53,75; Canaã dos Carajás, Serra do Cristalino (CGC 01): -6,41 -49,79; Ilha do Marajó, Caldeirão (BMNH 23.8.9.9 [holotype of *maraxina*]) (Only Photos): -0,62 -51,05; Itaituba (MPEG 15234, 15235), BR-165, estrada Santarém-Cuiabá, Km 446 (MPEG 12736, 12746 – 12748, 12932, 12933, 12941, 12943, 12946 – 12950), BR-165, estrada Santarém-Cuiabá, Km 446, Rio Jamanxizinho (USNM 546192 – 546208), BR-165, estrada Santarém-Cuiabá, Km 448 (MPEG 12737, 12928, 12944, 12945): -4,92 -55,6, Itaituba-Altamira, Km 25 (USNM 543299 – 543301): -4,33 -55,67;

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Itaituba-Jacareacanga, Km 19 (USNM 461664, 461665): -4,3 -56,2; Jacareacanga, Floresta Nacional do Crepori, Creporizão (CT 12): -6,56 -57; Jacareacanga, Floresta Nacional do Crepori, Rio do Coxo (CT 15): -7,24 -57,11; Marabá, Serra dos Carajás (MPEG 11824): -6,26 -50,27; Marabá, Serra dos Carajás (IAVRD 114), Noroeste II (MPEG 38928, 38955), Serra Sul corpo A (MPEG 38948, 38988), Barragem da Pêra (MPEG 38974, 38985), N5E (MPEG 38956), Bloco 3 (MPEG 38953): -6 -50,21; Mojuí dos Campos (MPEG 12586, 12742, 12743,USNM 545583): -2,6 -54,71; Santarém, Curuá-Una (MPEG 11841, 11842, 15415 – 15421): -2,83 -54,37; Santarém, BR-165, estrada Santarém-Cuiabá (MPEG 8091), Santarém, BR-165, estrada Santarém-Cuiabá, km 212 (MPEG 8678, USNM 544480), km 216 (MPEG 8092, 12717, 15236 – 15238, USNM 544486), km 217 (MPEG 8082 – 8088, 8679, 8681, 15225, USNM 544478, 544479, 544481 – 544485, 544487 – 544495): -4, -54,67; Santarém, BR-165, estrada Santarém-Cuiabá, Km 82 (MPEG 15230), km 84 (MPEG 8089, 15231 – 15233, USNM 461666 - 461670): -3,02 -54,96; Santarém, Belterra (MPEG 11840): -2,65 -54,95; Santarém, Taperinha (MPEG 313, 3381 – 3385, 5022 – 5025, MZUSP 3693): -2,53 -54,28; São Félix do Xingu, Gorotire, Rio Fresco (MZUSP 9931): -6,65 -51,98; São Félix do Xingu, Nilo Peçanha, afluente esquerdo Rio Fresco (MPEG 1318): -7,83 -51,5; São João do Araguaia, Fazenda São Raimundo (MPEG 10134): -5,36 -48,79; Vitória do Xingu, Bom Jardim (BML 734, MPEG 39750, 39757, 39771, 39780, 39784, 39786, 39813): -3,4 -51,75; *Rondônia*, Campo Novo de Rondônia, Pacaás Novos (MPEG 39067, 39083, 39097, 39107 – 39110, 39112, 39115, 39120 – 39123, 39133, 39140, 39150 – 39152, 39181, 39192, 39202, 39206, 39216, 39217): -10,48 -62,48; Ouro Preto D'Oeste, (MPEG 16116): -10,66 -62,3; Santa Bárbara (MZUSP 20082, 20089, 20093): -9,2 -62,9; Vilhena, Fazenda Cachoeira (MPEG 34932, 34934): -12,72 -60,12.

Monodelphis palliolata: **VENEZUELA** – *Aragua*, Est. Biol. Rancho Grande, 13 Km NW Maracay (USNM 517244 – 517246, 517248 – 517251): 10,35 -67,67; Guamita, 8 Km NW Maracay (USNM 517247): 10,32 -67,63; Ocumare De La Costa, 3 Km S (USNM 517242, 517243): 10,4 -67,77; *Barinas*, Altamira (USNM 418492 – 418494, 418496, 418497): 8,83 -70,5; *Carabobo*, Las Quiguas (USNM 296801): 10,4 -68; Montalban (USNM 418486, 418489), Montalban, 1 Km E, Sanjon (USNM 418485), Montalban, 1 Km S, Hato Laredo (USNM 418490, 418491), Montalban, 1 Km SE, El Merey (USNM 418487, 418488): 10,2 -68,33; Montalban, 4.5 Km SE, Sabana Aguirre (USNM 418484): 10,18 -68,3; Urama, 10 Km NW, El Central (USNM 372920, 372921): 10,53 -68,38; *Distrito Federal*, Hda. Carapiche, near El Limón, 48 Km W Caracas (USNM 385003): 10,48 -67,32; San Julian (USNM 143800): 10,62 -66,83; *Falcon*, Boca De Yaracuy, 28 Km WNW Pto. Cabello (USNM 371282): 10,58 -68,25, near La Pastora, 14 Km ENE Mirimire (USNM 418469, 418470, 418474 – 418476, 418478): 11,2 -68,62; near Mirimire (USNM

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406905): 11,17 -68,73; Urama, 19 Km NW, Km 40 (USNM 372917): 10,62 -68,4; *Guárico*, Parque Nac. Guatopo, 15 Km NW Altagracia (USNM 385006): 9,97 -66,42; *Merida*, La Azulita (FMNH 22180 – 22182): 8,72 -71,45; *Miranda*, Birongo (USNM 416935): 10,48 -66,27; Curupao, 5 Km NNW Guarenas (USNM 385007, 385100): 10,52 -66,63; Río Chico, 6 Km SSE (USNM 385008, 385009, 385012, 385013): 10,27 -65,97; *Monagas*, Caripito (AMNH 142610): 10,13 -63,1; Río Cocollar (AMNH 69942): 10,17 -63,78; *Sucre*, Manacal, 26 Km ESE Carupano (USNM 406903, 406904): 10,62 -63,02; *Táchira*, San Juan de Colón (FMNH 20524 [holotype of *palliolatus*]) (Only Photos): 8.03 -72.26; *Trujillo*, La Ceiba, 52 Km WNW Valera (USNM 371293, 371294): 9,52 -71,05; Valera, 12 Km WNW, near Isnoto (USNM 370015, 370016): 9,35 -70,7; Valera, 19 Km N, near Agua Viva (USNM 371285): 9,52 -70,67; Valera, 23 Km NNW, Motatan river (USNM 371283), 25 Km NW, near Agua Santa (USNM 370013): 9,53 -70,67; Valera, 30 Km NW, near El Dividive (USNM 371289, 371291): 9,52 -70,73; *Yaracuy*, Minas De Aroa, 20 Km NW San Felipe (USNM 418479 – 418482, 490237): 10,42 -68,9; *Zulia*, Kasmera, 21 Km SW Machiques (USNM 418483, 490238): 9,98 -72,72; Mision Tukuko (USNM 448513 – 448518, 448751): 9,83 -72,87; Sierra de Perija, Río Cogollo (FMNH 22178, 22179): 10,43 -72.

Monodelphis sp. nov. "touan sul": BRASIL – *Pará*, Altamira, Cachoeira do Espelho, east bank Rio Xingu, 52 km SSW Altamira (MZUSP 21284, 21285, USNM 549279, 549280): -3,65 -52,37; Anapu, Caracol (MPEG 39814, 39762, 39779, 39788, 39789): -3,45 -51,68; Cametá, Rio Tocantins (FMNH 140784): -2,25 -49,5; Marabá, Floresta Nacional do Tapirapé Aquiri, Área Controle 1, Igarapé Cotia (PSA 61, 63, 116): -5,85 -50,54; Marabá, Floresta Nacional de Tapirapé Aquiri, Barragem de Finos (PSA 140): -5,82 -50,49; Marabá, Floresta Nacional de Tapirapé Aquiri, Barragem de Rejeitos (PSA 44, 45, 158): -5,77 -50,51; Marabá, Floresta Nacional de Tapirapé Aquiri, Igarapé Mano (PSA 169, 187): -5,77 -50,56; Marabá, 26 Km N e 30 km W, near Itupiranga (MPEG 10248, 10249, 11698, 11699): -5,1 -49,4; Marabá, 73 Km N e 45 km W, near Jatobal (MPEG 10247, 11289 – 11293, USNM 519725, 519726, 521432): -4,68 -49,53; Ilha do Marajó, Chaves, Fazenda Tauari (MAJ 37, 42, 43): -0,42 -49,98; Portel, Floresta Nacional de Caxiuanã, Igarapé Caquajó (CAX 74, 126, 170, 180, 313, 326, 327, 335, 359, 417, 470, 593, 602, 630, 645, MAR 159, 200, 218, 272, 374, 375, 422, 427, 872, 880, 919, 1023, 1049, 1121, 1130, 1151, 1200, 1205, 1288, 1312, 1395): -1,96 -51,62; Porto de Moz (AMNH 95976): -1,75 -52,23; São Geraldo do Araguaia, Serra das Andorinhas (MPEG 25402): -6,4 -48,53; Tucuruí, Vila Permanente (MPEG 12405): -3,7 -49,7.

Monodelphis. sp. nov. "Trombetas": BRASIL – *Amazonas*, Itacoatiara (FMNH 20134, MPEG 7243, MZUSP 4513): -3,13 -58,42; Itacoatiara, Igarapé Anibá (MZUSP 5648): -2,92 -58,55;

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Manaus (MN 16802, 16804, MPEG s/nº): -3,13 -60,02; Manaus, 80 Km N (USNM 579976 – 579979): -2,42 -59,83; Santo Antônio de Amatary (AMNH 92879): -2,6 -56,73; *Pará,* Alenquer, Grão Pará Sul (CN 166): -0,15 -55,18; Faro, Floresta Estadual de Faro (CN 52): -1,7 -57,2; Faro, Rio Jamundá, Castanhal (AMNH 93972, 93973, 94161): -2,18 -56,73; Oriximiná, Cachoeira Porteira (MPEG 10035, 10037 – 10048, 10260 – 10265, 12739 – 12741, 12744, 12927, 12930, 12931, 12936, 12942, 12951, 12741, 12927, 12951, USNM 546209 - 546219): -1,03 -57,15; Oriximiná, Porto Trombetas, Igarapé Greig (MPEG 39811, 39812): -1,84 -56,53; Oriximiná, Porto Trombetas, Platô Bacaba (SLF 216, 244, 325, 335, 337): -1,77 -56,37; Oriximiná, Porto Trombetas, Platô Bela Cruz, 40 km Sw (MPEG 38093, BAC 215, BAC 230): -1,80 -56,51; Oriximiná, Porto Trombetas, Platô Cipó (MPEG 39810): -1,73 -56,61; Oriximiná, Porto Trombetas, Platô Greig, 43 km SW (MPEG 38052, 38054, 38056, 38074, 38095, BAC 228, 229, 236, 237): -1,83 -56,42; Oriximiná, Porto Trombetas, Platô Saracá (MPEG 39815): -1,69 -56,5; Oriximiná, Porto Trombetas, Platô Teófilo (MG 38063, BAC 231, 233): -1,77 -56,57; Tiriós, Rio Paru, 12 Km Surinam, Serra Do Tumucumaque (USNM 392044 – 392049): 2,5 -56; *Roraima,* São João da Baliza, UHE Alto Jatapu (MN 51660): 0,93 -59,9. **GUYANA – *Potaro-Siparuni*** (F-43457 – Only Photos), Anundebaru (AMNH 75830, 75831): 4,86 -59,22; Minehaha Creek (AMNH 36317): 5,13 -59,12. **SURINAME – *Brokopondo*,** Finisanti, Saramacca River (FMNH 95338): 5,13 -55,48; *Marowijne,* Moengo (USNM 238114): 5,62 -54,4; *Paramaribo* (USNM 319939, 319940): 5,83 -55,17; *Saramacca*, La Poule (FMNH 95339): 5,78 -55,42; *Sipaliwini*, Paloemeu Airstrip (FMNH 94018, 94019): 3,35 -55,45.

Monodelphis **"species A":** **VENEZUELA – *Guárico*,** Estación Biológica De Los Llanos, 9 Km SE Calabozo (USNM 443776, 443780, 490240), 7 to 10 Km S and 5 Km E Calabozo (USNM 443774, 443775, 443777, 443780): 8,87 -67,38.

Monodelphis **sp. "Manaus":** **BRASIL – *Amazonas*,** Manaus, Conjunto Parque do Rouxinol (INPA 2854) (Only Photos): -3,13 -60,01.

Monodelphis domestica: **BRASIL – *Mato Grosso*,** Cuiabá (BMNH 87.10.25.1 [holotype of *domestica*]) (Only Photos); *Piauí,* Brasileira, Parque Nacional de Sete Cidades (LZUFPI 1098), Castelo do Piauí, Fazenda Bonito (LZUFPI 201), José de Freitas, Nazareth Eco (LZUFPI 158), União, Povoado São Vicente, Sítio Ouro Verde (LZUFPI 146); *Tocantins*, Palmeirante, Fazenda Taboca (MPEG 34983), Serra de Jaraguá, Fazenda Nova (MPEG 34994).

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Unidentified Specimens *:*

BRASIL – *Pará*, Monte Alegre, Serra do Ererê (MPEG 34583); Monte Dourado, 50 Km W de Monte Dourado (MN 24086, 24087): These specimens are from localities placed between the distribution area of *M.* sp. nov. "Trombetas" and *M. touan*, and could not be positively associated to any of these two species. The specimen MPEG 34583 is a skin of an apparent early adult male, which shows external features of both species. The specimen MN 24086 is a skin/skull of an aduld male, and MN 24087 is a juvenile; both of them fit better the morphology of *M.* sp. nov. "Trombetas", but because they exhibit much faded skins, their color may had been altered, what prevent us of a secure identification.

BRASIL – *Pará*, Marabá, Serra Norte (USNM 543302): Only a skull of this juvenile specimen was available, and we were not able to allocate it neither in *Monodelphis girina* nor in *Monodelphis* sp. nov. "touan sul", both of these species potentially occurring at this locality.

BRASIL – *Roraima*, Limão, Rio Cotinga (AMNH 75520): This specimen was not allocated in any morphotype analyzed by us. It is an old adult male, skin and skull, which proved to be externally similar to paler specimens of *M. glirina*, but showed important cranial differences from this species and others herein analyzed.
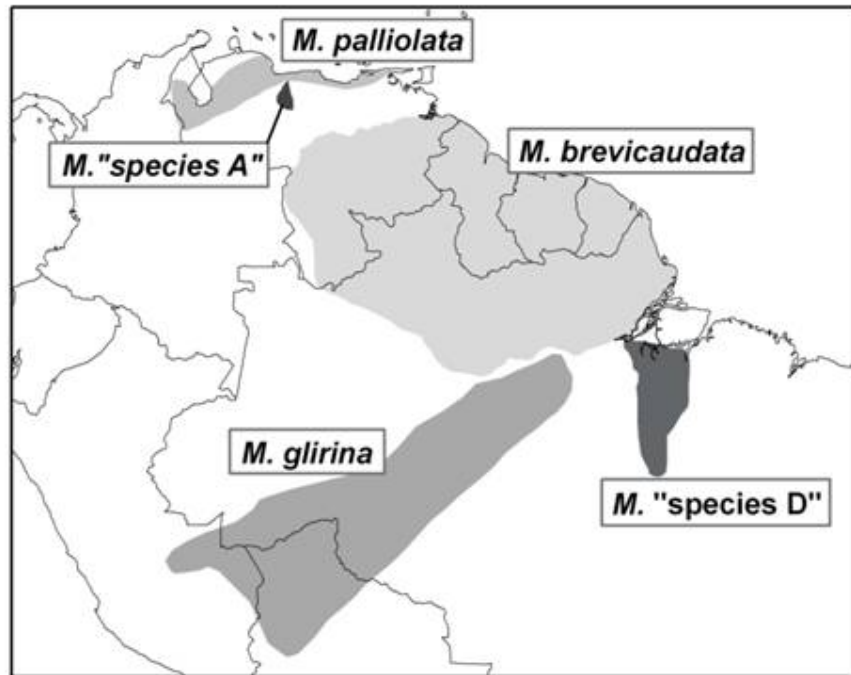
Figure 1. Geographic distributions of species of the *Monodelphis brevicaudata* complex based on earlier studies. This figure was modified from Pine & Handley, 2007.
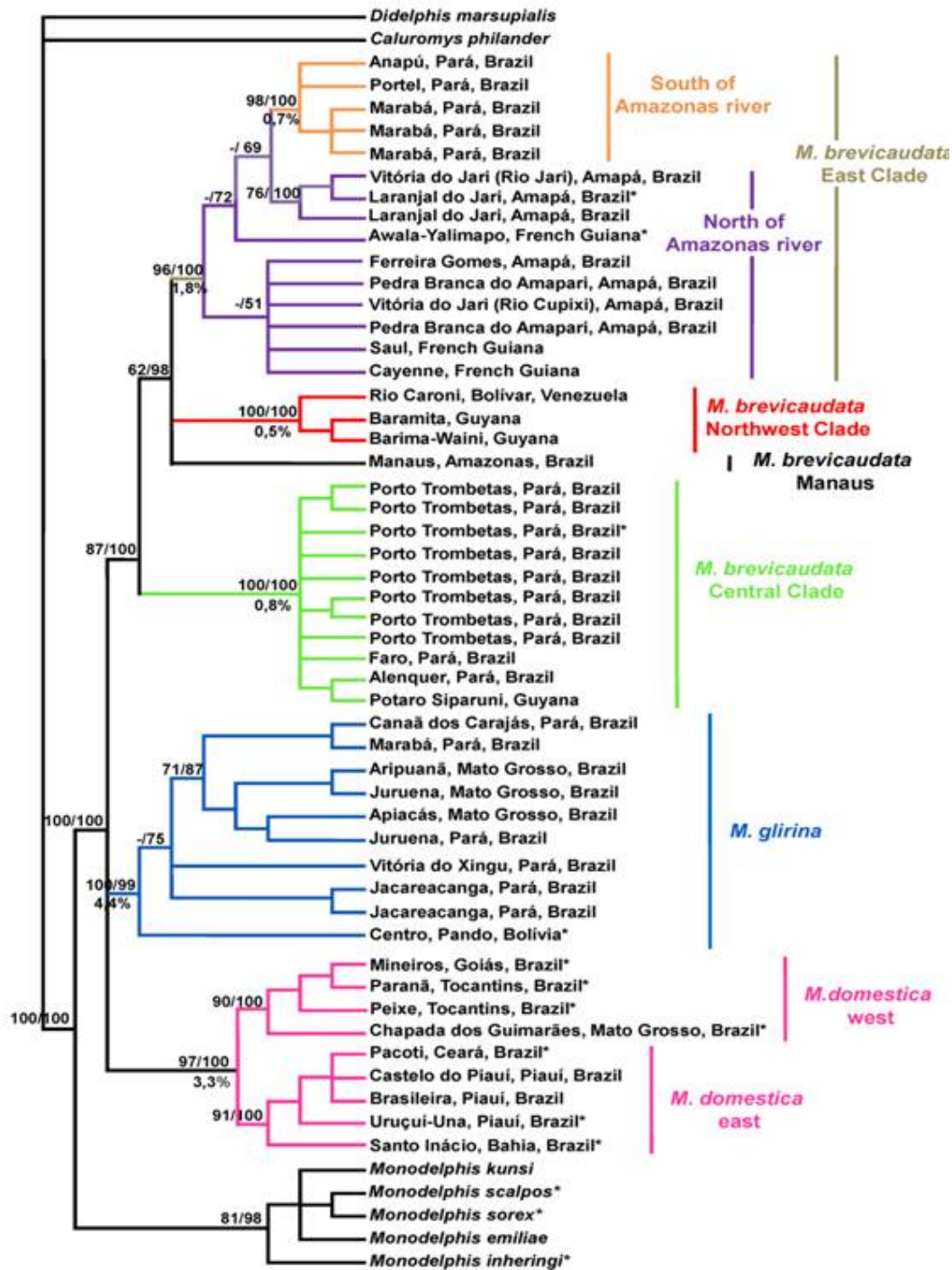
Figure 2. Phylogenetic relationships of species of the *M. brevicaudata* complex represented by the Bayesian tree resulting from the analysis of the combined matrices of 471 base pairs of the mitochondrial cytochrome *b* gene and 412 base pairs of the mitochondrial 16S rDNA gene. Numbers above branches represent parsimony and Bayesian posterior probabilities, respectively ('-' means a value lower than 50%). Numbers below branches correspond to average genetic distances among members of the clade. Asterisks refer to specimens/localities for which we did not examine.
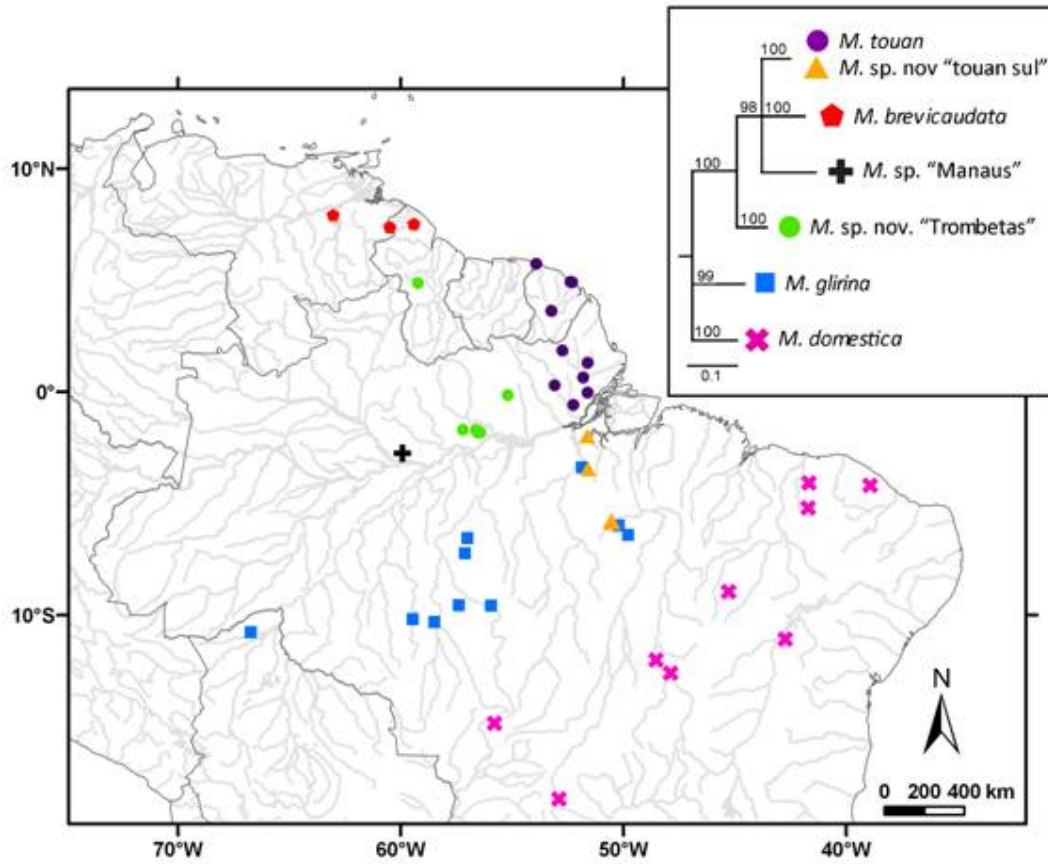
Figure 3. Collecting localities of specimens sampled in molecular analyses, and corresponding clade structure found in the molecular phylogeny, whit taxon names associated to them (tree to the right). Numbers above branches on the phylogeny represent Bayesian posterior probabilities.

Figure 4. Dorsal views of the skins of adult specimens of (top to bottom): *M. glirina* (USNM 521429), *M. palliolata* (USNM 406904), *M. brevicaudata* (USNM 385005), *M.* sp. nov. "Trombetas" (BAC 237, paratype); *M. touan* (IEPA 1154); *M.* sp. nov "touan sul" (MAR 880, holotype). Scale bar = 50 mm.
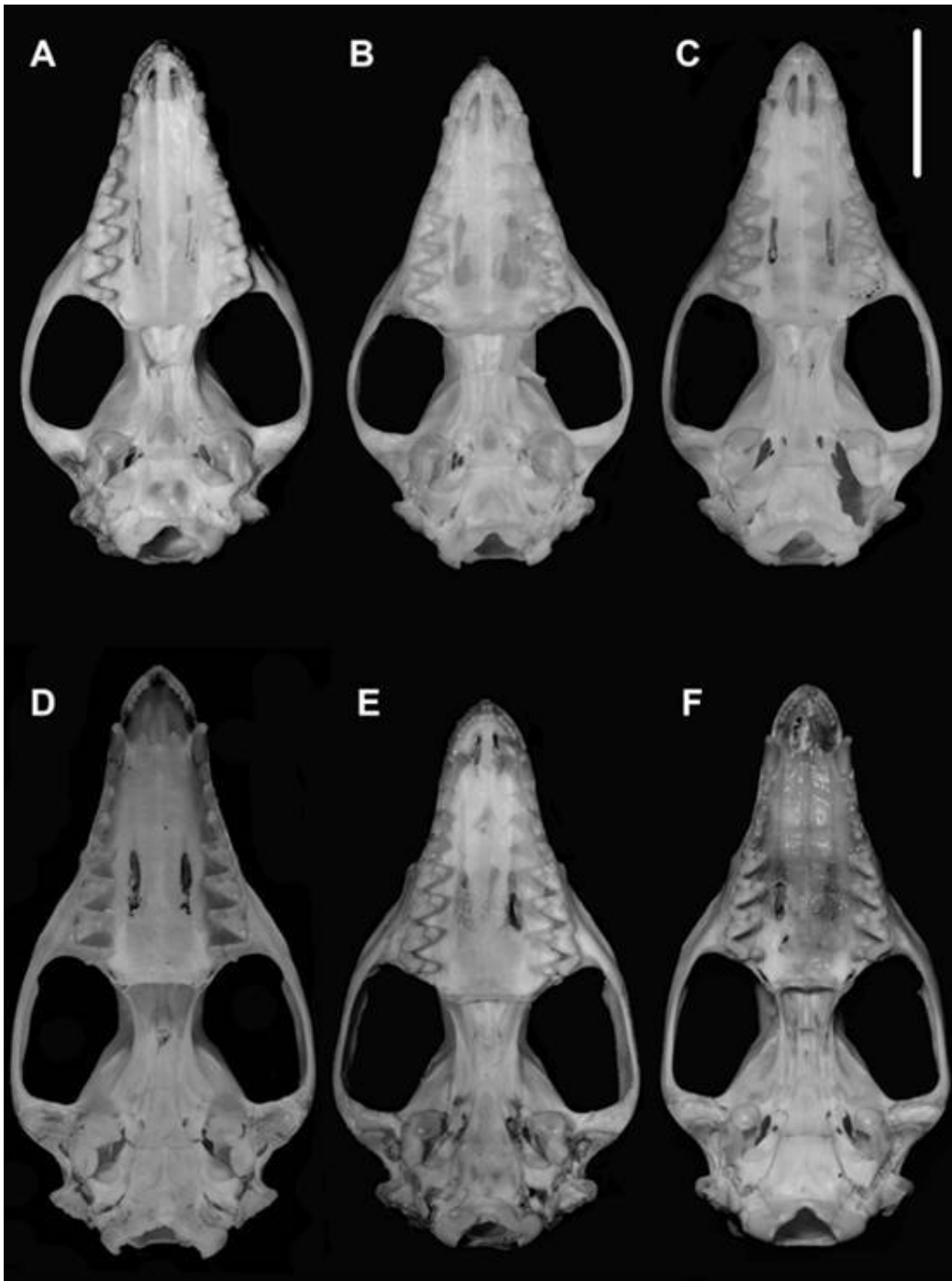
Figure 5. Ventral views of the skins of adult specimens of six different species recognized in this study. Top to bottom: *M. glirina* (USNM 521429), *M. palliolata* (USNM 406904), *M. brevicaudata* (USNM 385005), *M.* sp. nov. "Trombetas" (BAC 237, paratype), *M. touan* (IEPA 1154), *M.* sp. nov. "touan sul" (MAR 880, holotype). Scale bar = 50 mm.

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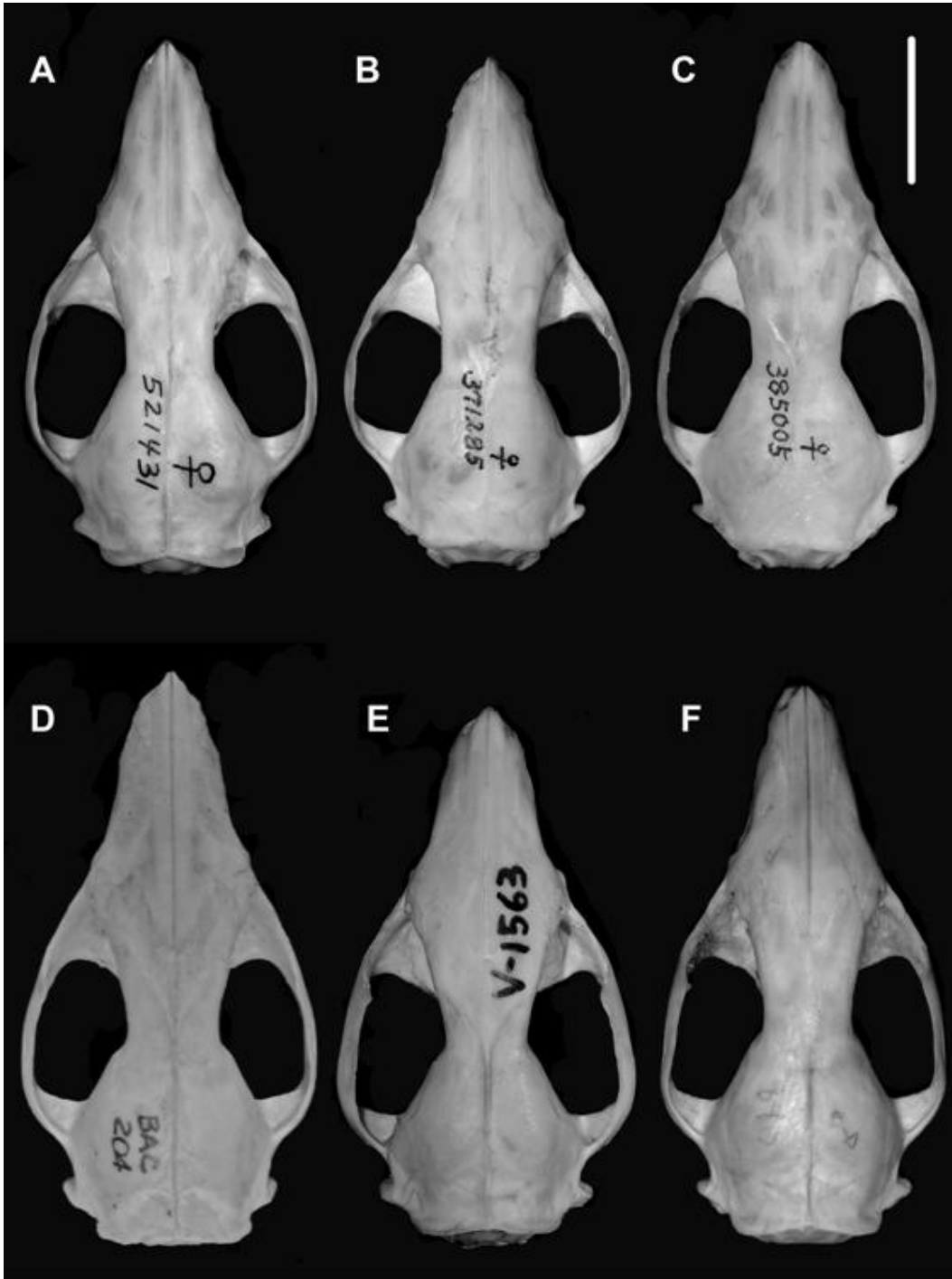
Figure 6. Dorsal views of the skulls of old adult specimens of six different species recognized in this study. **A**, *M. glirina* (USNM 521431, female); **B**, *M. palliolata* (USNM 371285, female); **C**, *M. brevicaudata* (USNM 385005, female); **D**, *M.* sp. nov. "Trombetas" (MPEG 38052, holotype, male); **E**, *M. touan* (ISEM V-1563, male); **F**, *M. touan sul* (MAR 880, holotype, male). Scale bar = 10 mm.
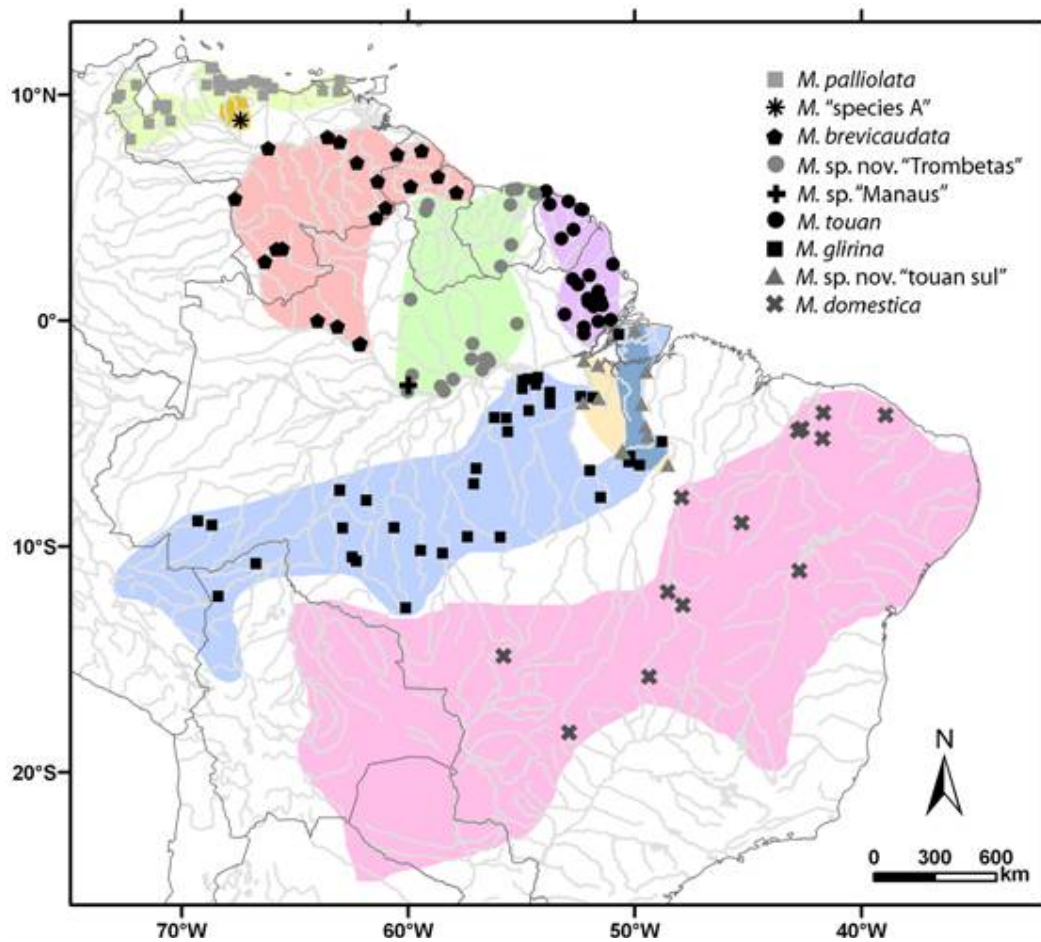
Figure 7. Ventral views of the skulls of old adult specimens of six different species recognized in this study. **A**, *M. glirina* (USNM 521431, female); **B**, *M. palliolata* (USNM 371285, female); **C**, *M. brevicaudata* (USNM 385005, female); **D**, *M.* sp. nov. "Trombetas" (MPEG 38052, holotype, male); **E**, *M. touan* (ISEM V-1563, male); **F**, *M. touan sul* (MAR 880, holotype, male). Scale bar = 10 mm.

Figure 8. Updated distribution of species of the *Monodelphis brevicaudata* complex recognized in this study. Species boundaries (shades) are based on our data and Pine & Handley, 2007. Points indicate collecting localities of specimens examined by us. *M. palliolata* also occurs in Colombia, but distribution in that country cannot be correctly drawn due to the absence of known precise localities (Pine & Handley, 2007).
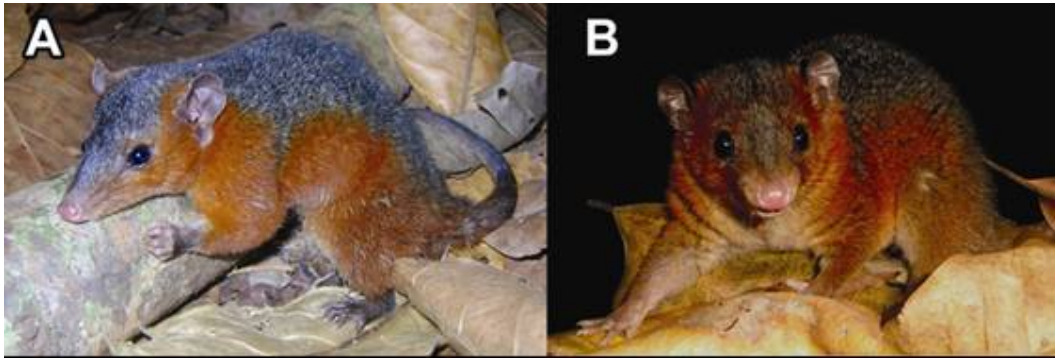
Figure 9. Adult males of two species recognized in this study: **A**, *Monodelphis* sp. nov. "touan sul" (PSA 187) from Floresta Nacional de Tapirapé Aquiri, Marabá, Pará, Brazil; **B**, *Monodelphis* sp. nov. "Trombetas" (SLF 325, paratype) from Porto Trombetas, Oriximiná, Pará, Brazil.
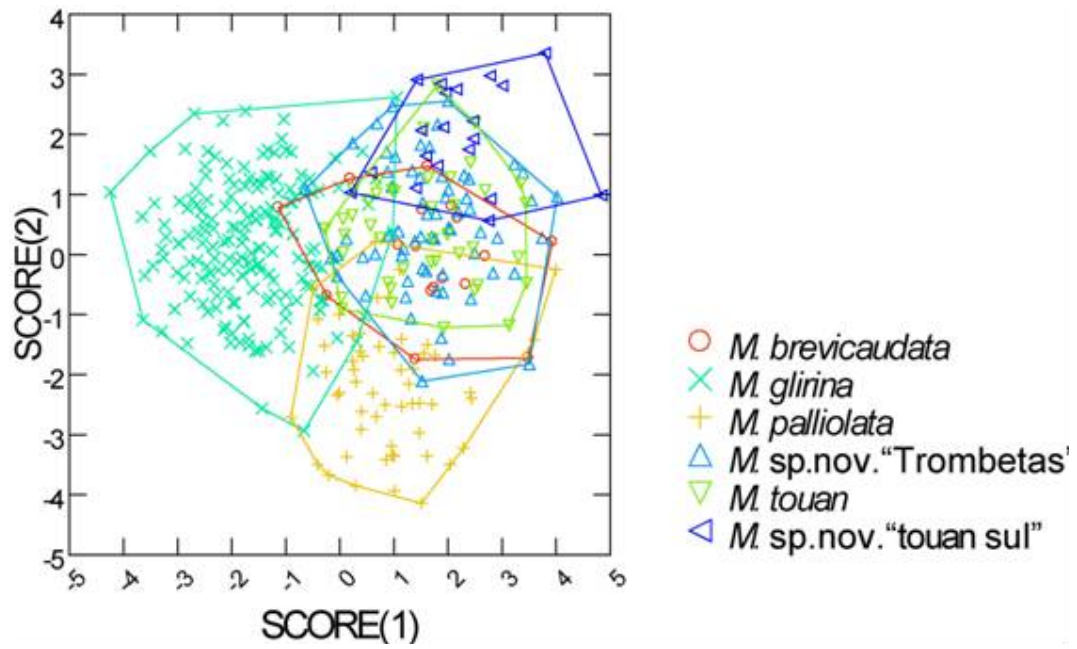
Figure 10. Bivariate scattergram from the canonical analysis of discriminance. Wilks' lambda = 0.093, F= 12.830, df= 1.696; p=0.000.

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TABLES

Table 1. Estimate of pairwise divergence of cytochrome b (475 pb) and 16S rDNA (410 pb) genes among *M. glirina*, *M. domestica*, and the four lineages found inside *M. brevicaudata* (sensu Voss *et al.*, 2001). The values inside brackets correspond to the average distance inside each group. Below the diagonal: values for cytochrome b (Tamura & Nei, α= 1.4187); Above the diagonal: values to 16S (Tamura & Nei, α= 0,1649).

Pairwise distance (cytb/16S)	Northwest clade (0.0036)	East clade (0.0059)	Central clade (0.0008)	*M. glirina* (0.0086)	*M. domestica* (0.0125)	Specimen from Manaus (--)
Northwest clade (0.005)		0.032	0.032	0.064	0.073	--
East clade (0.018)	0.069		0.042	0.082	0.075	--
Central clade (0.008)	0.082	0.065		0.075	0.053	--
M. glirina (0.044)	0.125	0.141	0.118		0.037	--
M. domestica (0.033)	0.114	0.098	0.091	0.131		--
Specimen from Manaus (--)	0.076	0.069	0.079	0.131	0.098	

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Table 2. Descriptive statistics for weight (g) and measurements (mm) of adult (age classes 5- 8) specimens in the *Monodelphis brevicaudata* complex species, grouped by sex (see text for character abbreviations). Measurements are shown as Mean ± Standard Deviation (sample size)/ Range.

SEX	CHARACTER	SPECIES					
		M. brevicaudata	*M.* sp. nov. "Trombetas"	*M. touan*	*M.* sp. nov."touan sul"	*M. glirina*	*M. palliolata*
♂	Weight	96 ± 24 (4)/ 70 - 127	77 ± 16 (27)/ 38 - 105	82 ± 10 (21)/ 64 - 100	68 (1)	86 ± 24 (61)/ 44 - 150	75 ± 18 (19)/ 49 - 106
	TL	243 ± 13 (5)/ 228 - 262	232 ± 18 (19)/ 197 - 262	251 ± 10 (5)/ 235 - 260	242 ± 17 (3)/ 227 - 260	242 ± 20 (47)/ 195 - 280	241 ± 21 (32)/ 193 - 288
	HBL	157 ± 12 (6)/ 143 - 170	149 ± 13 (32)/ 120 - 182	159 ± 8 (23)/ 138 - 170	155 ± 13 (3)/ 144 - 169	153 ± 14 (76)/ 120 - 180	152 ± 13 (33)/ 123 - 183
	LT	83 ± 11 (6)/ 64 - 97	83 ± 6 (31) 70 - 98	88 ± 5 (22)/ 79 - 95	88 ± 4 (3)/ 83 - 91	88 ± 9 (76)/ 65 - 106	89 ± 9 (33)/ 70 - 105
	HF	24 ± 2 (6)/ 21 - 25	23 ± 2 (31)/ 19 - 28	24 ± 2 (23)/ 20 - 26	24 ± 1 (4)/ 24 - 25	22 ± 2 (75)/ 18 - 26	23 ± 2 (33)/ 18 - 25
	Ear	21 ± 2 (4)/ 18 - 23	19 ± 2 (29)/ 13 - 23	19 ± 1 (23)/ 18 - 23	21 ± 1 (2)/ 20 - 21	20 ± 2 (76)/ 15 -22	21 ± 2 (30)/ 17 - 28
	GLS	39.0 ± 3.4 (6)/ 34.7 - 44.5	38.4 ± 2.1 (35)/ 33.8 - 42.3	39.8 ± 1.7 (25)/ 36.0 - 42.8	38.9 ± 1.7 (15)/ 36.5 - 41.8	39.5 ± 2.4 (85)/ 33.6 - 44.2	38.4 ± 2.2 (30)/ 34.3 - 44.1
	CBL	39.4 ± 3.6 (6)/ 35.1 - 45.3	38.5 ± 2.0 (33)/ 34.0 - 42.1	39.8 ± 1.6 (25)/ 36.6 - 42.8	38.9 ± 1.7 (15)/ 36.3 - 42.0	39.4 ± 2.4 (83)/ 33.4 - 44.2	38.4 ± 2.4 (31)/ 34.1 - 44.5
	RL	16.3 ± 1.7 (5)/ 14.1 - 18.6	16.0 ± 1.1 (29)/ 13.6 - 18.2	16.6 ± 0.7 (23)/ 15.2 - 17.9	16.1 ± 0.8 (14)/ 14.7 - 17.8	16.2 ± 1.1 (76)/ 12.9 - 18.4	15.9 ± 1.1 (27)/ 13.9 - 18.4
	NL	19.4 ± 2.5 (5)/ 16.4 - 22.9	18.7 ± 1.4 (30)/ 16.0 - 21.0	19.3 ± 1.0 (23)/ 17.2 - 20.9	18.5 ± 1.2 (14)/ 17.2 - 20.6	19.3 ± 1.5 (76)/ 15.4 - 22.6	18.7 ± 1.4 (27)/ 15.7 - 21.8
	PL	21.6 ± 1.7 (7)/ 19.3 - 24.7	21.2 ± 1.2 (35)/ 18.6 - 23.5	22.0 ± 1.0 (23)/ 20.4 - 22.0	21.5 ± 1.0 (15)/ 20.4 - 23.3	22.0 ± 1.3 (79)/ 18.3 - 24.7	21.1 ± 1.2 (33)/ 18.8 - 24.1
	MTR	15.5 ± 0.9 (7)/ 14.2 - 16.5	15.4 ± 0.6 (36)/ 14.3 - 16.6	15.8 ± 0.4 (27)/ 14.8 - 16.5	15.8 ± 0.5 (15)/ 15.0 - 16.6	16.0 ± 0.7 (87)/ 14.0 - 17.2	15.1 ± 0.7 (33)/ 13.6 - 16.8
	UMS	7.9 ± 0.3 (7)/ 7.4 - 8.4	7.9 ± 0.3 (35)/ 7.3 - 8.5	8.0 ± 0.3 (26)/ 7.4 - 8.4	8.2 ± 0.3 (15)/ 7.5 - 8.7	8.2 ± 0.3 (85)/ 7.3 - 9.0	7.6 ± 0.2 (33)/ 7.2 - 8.0
	LUI	2.1 ± 0.1 (7)/ 2.0 - 2.3	2.0 ± 0.1 (34)/ 1.8 - 2.4	2.1 ± 0.1 (26)/ 1.9 - 2.3	2.1 ± 0.1 (15)/ 1.9 - 2.2	2.1 ± 0.2 (81)/ 1.7 - 2.6	2.0 ± 0.1 (32)/ 1.9 - 2.1
	LM3	2.3 ± 0.1 (7)/ 2.2 - 2.4	2.3 ± 0.1 (36)/ 2.1 - 2.6	2.4 ± 0.1 (27)/ 2.1 - 2.6	2.4 ± 0.1 (15)/ 2.2 - 2.6	2.5 ± 0.1 (86)/ 2.1 - 2.8	2.3 ± 0.1 (33)/ 2.1 - 2.4
	WM3	2.7 ± 0.1 (7)/ 2.5 - 2.8	2.7 ± 0.1 (36)/ 2.5 - 2.9	2.7 ± 0.1 (27)/ 2.5 - 2.9	2.8 ± 0.1 (15)/ 2.5 - 3.0	2.8 ± 0.1 (87)/ 2.5 - 3.2	2.6 ± 0.1 (33)/ 2.3 - 2.9
	WM4	3.0 ± 0.2 (7)/ 2.8 - 3.2	3.0 ± 0.1 (36)/ 2.7 - 3.2	3.0 ± 0.1 (27)/ 2.7 - 3.3	3.1 ± 0.1 (15)/ 2.7 - 3.2	3.0 ± 0.1 (87)/ 2.6 - 3.4	2.9 ± 0.1 (33)/ 2.7 - 3.1
	HC	4.2 ± 0.9 (7)/ 3.0 - 5.3	4.2 ± 0.6 (36)/ 3.0 - 5.2	4.3 ± 0.5 (27)/ 3.4 - 5.6	4.0 ± 0.4 (15)/ 3.4 - 4.8	4.3 ± 0.8 (87)/ 2.8 - 6.1	4.6 ± 0.6 (33)/ 3.5 - 5.7
	PBM3	12.0 ± 0.5 (7)/ 11.1 - 12.6	11.9 ± 0.4 (35)/ 11.1 - 12.8	12.1 ± 0.4 (26)/ 11.4 - 12.7	12.0 ± 0.4 (15)/ 11.3 - 12.7	12.4 ± 0.5 (87)/ 10.7 - 13.7	11.7 ± 0.5 (33)/ 10.5 - 13.0
	PPB	4.0 ± 0.2 (7)/ 3.5 - 4.2	3.9 ± 0.2 (33)/ 3.4 - 4.6	4.0 ± 0.2 (24)/ 3.5 - 4.6	4.0 ± 0.2 (14)/ 3.6 - 4.3	3.9 ± 0.3 (81)/ 3.3 - 4.7	3.9 ± 0.2 (32)/ 3.6 - 4.4
	BFO	4.9 ± 0.4 (6)/ 4.3 - 5.3	4.9 ± 0.3 (34)/ 4.2 - 5.6	5.0 ± 0.3 (20)/ 4.3 - 5.5	4.9 ± 0.2 (15)/ 4.5 - 5.1	4.7 ± 0.4 (86)/ 3.8 - 5.6	4.5 ± 0.4 (30)/ 3.9 - 5.4
	BPG	12.4 ± 0.8 (6)/ 11.0 - 13.2	12.1 ± 0.5 (35)/ 11.1 - 13.1	12.1 ± 0.4 (26)/ 11.4 - 13.1	12.2 ± 0.5 (15)/ 11.6 - 13.4	12.4 ± 0.7 (87)/ 11.1 - 14.2	11.8 ± 0.7 (33)/ 10.8 - 13.4
	LTB	5.7 ± 0.2 (6)/ 5.4 - 6.1	5.6 ± 0.2 (33)/ 5.1 - 6.4	5.7 ± 0.2 (26)/ 5.2 - 6.1	5.7 ± 0.2 (15)/ 5.5 - 6.3	5.8 ± 0.2 (85)/ 5.2 - 6.3	5.7 ± 0.3 (32)/ 5.2 - 6.6

Table 2. Continued.

SEX	CHARACTER	M. brevicaudata	M. sp. nov. "Trombetas"	M. touan	M. sp. nov."touan sul"	M. glirina	M. palliolata
				SPECIES			
	LIF	3.0 ± 0.3 (7)/ 2.5 - 3.6	2.8 ± 0.3 (31)/ 2.1 - 3.4	3.0 ± 0.3 (24)/ 2.3 - 3.8	2.6 ± 0.2 (15)/ 2.0 - 3.1	2.9 ± 0.3 (78)/ 1.3 - 3.5	3.0 ± 0.3 (32)/ 2.6 - 3.5
	BIF	0.7 ± 0.1 (7)/ 0.5 - 0.8	0.7 ± 0.1 (31)/ 0.5 - 0.8	0.7 ± 0.1 (24)/ 0.5 - 0.8	0.7 ± 0.1 (15)/ 0.5 - 0.8	0.6 ± 0.1 (76)/ 0.4 - 1.1	0.6 ± 0.1 (33)/ 0.5 - 0.8
	LMP	4.5 ± 0.3 (7)/ 4.1 - 5.0	4.5 ± 0.5 (34)/ 3.7 - 5.6	4.6 ± 0.7 (24)/ 2.4 - 5.9	4.2 ± 0.5 (14)/ 3.5 - 5.3	5.1 ± 0.5 (80)/ 3.8 - 6.2	4.9 ± 0.4 (31)/ 3.9 - 5.9
	BMF	0.6 ± 0.1 (7)/ 0.5 - 0.8	0.6 ± 0.1 (33)/ 0.4 - 1.0	0.7 ± 0.1 (24)/ 0.4 - 1.1	0.7 ± 0.2 (14)/ 0.5 - 1.2	0.6 ± 0.1 (79)/ 0.4 - 0.8	0.6 ± 0.1 (32)/ 0.4 - 0.8
	NB	6.4 ± 1.0 (7)/ 5.2 - 7.8	6.2 ± 0.7 (35)/ 4.8 - 8.3	6.5 ± 0.5 (26)/ 5.6 - 7.4	6.7 ± 0.5 (15)/ 5.8 - 7.6	6.1 ± 0.6 (86)/ 4.7 - 7.7	6.2 ± 0.6 (33)/ 5.4 - 7.4
	BRC	6.9 ± 0.8 (7)/ 6.1 - 8.3	6.8 ± 0.5 (35)/ 5.9 - 8.0	7.0 ± 0.5 (25)/ 6.3 - 8.0	6.8 ± 0.5 (15)/ 6.2 - 7.6	7.0 ± 0.7 (86)/ 5.7 - 8.6	6.8 ± 0.6 (33)/ 5.7 - 8.2
	BRO	11.8 ± 0.9 (7)/ 10.2 - 13.0	11.7 ± 0.6 (35)/ 10.4 - 12.8	12.2 ± 0.6 (26)/ 11.3 - 13.4	11.9 ± 0.6 (15)/ 10.9 - 12.9	11.8 ± 0.8 (86)/ 9.9 - 13.7	11.4 ± 0.9 (33)/ 10.0 - 14.0
	POC	6.1 ± 0.3 (7)/ 5.7 - 6.4	6.1 ± 0.3 (36)/ 5.6 - 6.6	6.1 ± 0.3 (26)/ 5.7 - 6.8	6.2 ± 0.2 (15)/ 5.9 - 6.5	6.0 ± 0.3 (86)/ 5.2 - 6.7	6.2 ± 0.2 (33)/ 5.8 - 6.5
	BBC	13.9 ± 1.0 (6)/ 12.4 - 15.5	13.6 ± 0.6 (34)/ 12.4 - 15.3	13.6 ± 0.5 (26)/ 12.8 - 14.8	13.7 ± 0.4 (15)/ 13.1 - 14.6	13.4 ± 0.7 (84)/ 11.9 - 15.3	13.4 ± 0.6 (31)/ 12.3 - 15.0
	ZB	21.4 ± 2.1 (6)/ 18.7 - 24.4	20.9 ± 1.4 (34)/ 17.7 - 23.7	21.4 ± 1.0 (26)/ 19.5 - 23.0	20.6 ± 1.0 (15)/ 19.1 - 22.3	21.7 ± 1.6 (85)/ 18.1 - 26.1	21.0 ± 1.7 (32)/ 17.6 - 25.7
	LM	29.2 ± 2.6 (7)/ 26.2 - 33.9	29.0 ± 1.8 (36)/ 25.5 - 32.0	30.0 ± 1.4 (27)/ 27.5 - 32.5	29.2 ± 1.5 (14)/ 27.1 - 31.9	30.1 ± 2.0 (86)/ 25.2 - 34.4	28.9 ± 1.9 (33)/ 25.2 - 33.6
	HMB	3.6 ± 0.4 (7)/ 3.2 - 4.2	3.6 ± 0.6 (36)/ 3.0 - 4.2	3.7 ± 0.2 (27)/ 3.3 - 4.1	3.5 ± 0.2 (14)/ 3.2 - 3.9	3.8 ± 0.3 (86)/ 3.0 - 4.5	3.5 ± 0.3 (33)/ 2.8 - 4.4
	LTR	16.6 ± 0.7 (6)/ 15.7 - 17.7	16.5 ± 0.6 (36)/ 15.4 - 17.9	16.9 ± 0.5 (27)/ 15.8 - 17.8	17.0 ± 0.6 (14)/ 15.8 - 17.6	17.2 ± 0.7 (86)/ 14.9 - 18.3	16.4 ± 0.7 (33)/ 15.0 - 18.2
	LMS	8.8 ± 0.4 (6)/ 8.4 - 9.3	8.8 ± 0.4 (36)/ 7.2 - 9.4	8.8 ± 0.3 (27)/ 8.0 - 9.2	9.0 ± 0.6 (14)/ 7.1 - 9.4	9.2 ± 0.3 (86)/ 8.3 - 9.8	8.5 ± 0.2 (33)/ 7.9 - 10.0
♀	Weight	67 ± 10 (9)/ 50 - 81	55 ± 13 (26)/ 33 - 96	52 ± 8 (14)/ 40 - 66	–	60 ± 11 (50)/ 40 - 85	46 ± 9 (14)/ 32 - 63
	TL	220 ± 14 (8)/ 200 - 237	207 ± 18 (10)/ 165 - 223	219 ± 10 (10)/ 205 - 235	–	219 ± 14 (43)/ 180 - 247	204 ± 13 (19)/ 178 - 227
	HBL	142 ± 11 (9)/ 128 - 161	133 ± 11 (27)/ 95 - 150	137 ± 9 (16)/ 119 - 155	–	137 ± 10 (70)/ 110 - 165	127 ± 10 (19)/ 102 - 141
	LT	79 ± 5 (9)/ 71 - 87	78 ± 6 (27)/ 65 - 90	77 ± 6 (16)/ 65 - 85	–	80 ± 6 (71)/ 65 - 90	77 ± 7 (19)/ 55 - 88
	HF	22 ± 1 (9)/19 - 23	20 ± 2 (26)/ 18 - 26	22 ± 1 (16)/ 19 - 23	–	21 ± 1 (69)/ 17 - 24	20 ± 1 (19)/ 18 - 22
	Ear	20 ± 2 (9)/ 18 - 23	16 ± 3 (23)/ 13 - 21	18 ± 2 (16)/ 13 - 20	–	19 ± 2 (69)/ 14 - 22	19 ± 2 (17)/ 16 - 22
	GLS	35.8 ± 1.8 (10)/ 32.7 - 38.7	35.2 ± 1.2 (27)/ 32.7 - 36.7	35.6 ± 1.1 (17)/ 33.6 - 37.6	36.7 ± 1.3 (6)/ 35.2 - 38.1	36.6 ± 1.5 (79)/ 33.1 - 40.3	34.1 ± 1.4 (19)/ 31.7 - 36.6
	CBL	35.9 ± 1.9 (10)/ 32.7 - 38.9	35.0 ± 1.3 (25)/ 32.6 - 36.8	35.5 ± 1.1 (17)/ 33.6 - 37.5	36.7 ± 1.3 (6)/ 35.1 - 38.1	36.5 ± 1.6 (77)/ 33.1 - 40.5	34.2 ± 1.5 (19)/ 31.6 - 36.8
	RL	14.8 ± 0.8 (8)/ 13.9 - 16.4	14.6 ± 0.6 (25)/ 13.4 - 15.7	14.6 ± 0.7 (14)/ 13.7 - 16.0	15.1 ± 0.8 (5)/ 13.9 - 16.0	14.9 ± 0.7 (63)/ 13.3 - 16.7	13.9 ± 0.8 (14)/ 12.3 - 15.3
	NL	17.6 ± 0.9(8)/ 16.6 - 19.4	16.9 ± 0.8 (25)/ 15.4 - 18.4	16.9 ± 0.9 (14)/ 15.6 - 18.6	17.2 ± 0.8 (5)/ 16.1 - 18.2	17.4 ± 1.0 (63)/ 14.7 - 19.8	16.2 ± 0.9 (14)/ 14.0 - 17.7

Table 2. Continued..

SEX	CHARACTER	SPECIES					
		M. brevicaudata	*M.* sp. nov. "Trombetas"	*M. touan*	*M.* sp. nov."touan sul"	*M. glirina*	*M. palliolata*
	PL	19.9 ± 1.0 (10)/ 18.2 - 21.8	19.5 ± 0.6 (24)/ 17.9 - 20.4	19.7 ± 0.8 (17)/ 18.9 - 21.4	20.3 ± 0.8 (6)/ 19 - 21.2	20.3 ± 1.0 (77)/ 18.0 - 22.7	18.9 ± 0.8 (20)/ 17.4 - 20.4
	MTR	14.6 ± 0.5 (10)/ 14.0 - 15.6	14.5 ± 0.5 (31)/ 13.5 - 15.2	14.8 ± 0.4 (17)/ 14.3 - 15.5	15.2 ± 0.3 (6)/ 14.6 - 15.5	15.3 ± 0.5 (79)/ 13.9 - 16.3	14.1 ± 0.5 (21)/ 13.2 - 14.8
	UMS	7.8 ± 0.3 (10)/ 7.3 - 8.1	7.7 ± 0.3 (31)/ 7.1 - 8.2	7.8 ± 0.3 (17)/ 7.3 - 8.2	8.2 ± 0.2 (6)/ 7.9 - 8.4	8.1 ± 0.3 (79)/ 7.0 - 8.7	7.5 ± 0.2 (21)/ 7.0 - 7.8
	LUI	2.0 ± 0.1 (10)/ 1.9 - 2.2	2.0 ± 0.1 (29)/ 1.8 - 2.1	2.1 ± 0.1 (17)/ 1.9 - 2.2	2.1 ± 0.1 (6)/ 2.0 - 2.2	2.1 ± 0.1 (79)/ 1.8 - 2.4	2.0 ± 0.1 (21)/ 1.8 - 2.1
	LM3	2.3 ± 0.1 (10)/ 2.2 - 2.5	2.3 ± 0.1 (31)/ 2.0 - 2.6	2.3 ± 0.1 (17)/ 2.2 - 2.5	2.5 ± 0.1 (6)/ 2.3 - 2.6	2.5 ± 0.1 (79)/ 2.1 - 2.7	2.2 ± 0.1 (21)/ 2.0 - 2.5
	WM3	2.6 ± 0.1 (10)/ 2.5 - 2.9	2.6 ± 0.1 (31)/ 2.4 - 2.9	2.7 ± 0.1 (17)/ 2.5 - 2.8	2.7 ± 0.1 (6)/ 2.7 - 2.8	2.8 ± 0.1 (79)/ 2.5 - 3.1	2.6 ± 0.1 (21)/ 2.4 - 2.9
	WM4	2.8 ± 0.1 (10)/ 2.6 - 2.9	2.8 ± 0.1 (31)/ 2.4 - 3.2	2.9 ± 0.2 (17)/ 2.6 - 3.1	3.0 ± 0.1 (6)/ 2.8 - 3.1	2.9 ± 0.2 (79)/ 2.5 - 3.4	2.8 ± 0.1 (21)/ 2.5 - 3.1
	HC	3.1 ± 0.3 (10)/ 2.7 - 3.6	3.1 ± 0.2 (31)/ 2.6 - 3.5	3.0 ± 0.3 (17)/ 2.1 - 3.5	3.1 ± 0.2 (6)/ 3.0 - 3.4	3.2 ± 0.3 (79)/ 2.7 - 4.4	3.1 ± 0.3 (21)/ 2.6 - 3.5
	PBM3	11.7 ± 0.6 (10)/ 10.8 - 12.6	11.2 ± 0.5 (29)/ 10.4 - 12.1	11.5 ± 0.3 (16)/ 11.1 - 12.0	11.8 ± 0.3 (6)/ 11.5 - 12.1	12.1 ± 0.5 (79)/ 10.8 - 13.0	11.2 ± 0.5 (21)/ 10.6 - 12.1
	PPB	3.7 ± 0.2 (10)/ 3.4 - 4.0	3.9 ± 0.2 (30)/ 3.4 - 4.3	3.8 ± 0.2 (17)/ 3.5 - 4.1	3.9 ± 0.2 (6)/ 3.6 - 4.0	3.8 ± 0.2 (75)/ 3.2 - 4.5	3.8 ± 0.1 (21)/ 3.5 - 4.1
	BFO	4.4 ± 0.2 (10)/ 4.0 - 4.7	4.6 ± 0.3 (29)/ 3.8 - 5.4	4.5 ± 0.2 (16)/ 4.2 - 4.8	4.7 ± 0.2 (6)/ 4.4 - 5.0	4.4 ± 0.5 (79)/ 3.6 - 5.7	4.2 ± 0.3 (17)/ 3.8 - 4.8
	BPG	11.7 ± 0.6 (10)/ 10.7 - 12.7	11.4 ± 0.4 (30)/ 10.3 - 12.3	11.5 ± 0.3 (17)/ 11.0 - 11.9	11.6 ± 0.3 (6)/ 11.4 - 12.1	11.7 ± 0.5 (76)/ 10.6 - 13.4	11.0 ± 0.6 (20)/ 10.1 - 12.0
	LTB	5.5 ± 0.2 (10)/ 5.2 - 5.9	5.4 ± 0.2 (27)/ 4.8 - 5.8	5.4 ± 0.2 (16)/ 5.0 - 5.7	5.8 ± 0.1 (6)/ 5.6 - 5.9	5.6 ± 0.2 (76)/ 5.0 - 6.1	5.4 ± 0.2 (20)/ 5.1 - 5.7
	LIF	2.9 ± 0.2 (10)/ 2.5 - 3.3	2.7 ± 0.2 (29)/ 2.3 - 3.2	2.7 ± 0.2 (16)/ 2.3 - 2.9	2.6 ± 0.3 (6)/ 2.1 - 3.0	2.6 ± 0.3 (74)/ 1.9 - 3.2	2.7 ± 0.2 (21)/ 2.3 - 3.1
	BIF	0.7 ± 0.1 (10)/ 0.6 - 0.8	0.7 ± 0.1 (29)/ 0.5 - 0.9	0.7 ± 0.1 (15)/ 0.6 - 0.8	0.7 ± 0.1 (6)/ 0.6 - 0.8	0.6 ± 0.1 (76)/ 0.5 - 0.9	0.6 ± 0.1 (21)/ 0.4 - 0.8
	LMP	4.3 ± 0.4 (10)/ 3.5 - 5.1	4.3 ± 0.5 (27)/ 3.4 - 5.1	4.7 ± 0.5 (17)/ 4.0 - 5.9	4.2 ± 0.3 (5)/ 3.8 - 4.6	4.9 ± 0.5 (78)/ 3.5 - 6.1	4.3 ± 0.3 (21)/ 3.5 - 5.0
	BMF	0.6 ± 0.1 (10)/ 0.5 - 0.7	0.6 ± 0.1 (26)/ 0.4 - 1.1	0.7 ± 0.1 (17)/ 0.5 - 0.9	0.7 ± 0.2 (5)/ 0.6 - 1.1	0.6 ± 0.1 (77)/ 0.4 - 0.8	0.6 ± 0.1 (21)/ 0.4 - 0.8
	NB	5.9 ± 0.5 (10)/ 5.1 - 6.6	5.7 ± 0.5 (30)/ 4.7 - 6.8	5.7 ± 0.5 (17)/ 4.6 - 6.7	6.1 ± 0.1 (6)/ 6.0 - 6.3	5.6 ± 0.4 (79)/ 4.6 - 6.7	5.4 ± 0.4 (21)/ 4.3 - 6.2
	BRC	6.1 ± 0.5 (10)/ 5.2 - 6.6	5.9 ± 0.4 (30)/ 5.2 - 6.6	5.8 ± 0.3 (17)/ 5.4 - 6.4	6.0 ± 0.1 (6)/ 5.9 - 6.2	6.2 ± 0.5 (79)/ 5.3 - 7.5	5.8 ± 0.4 (21)/ 5.0 - 6.4
	BRO	10.9 ± 0.7 (10)/ 9.9 - 11.9	10.8 ± 0.5 (29)/ 9.5 - 12.0	10.6 ± 0.5 (16)/ 9.9 - 11.7	11.0 ± 0.5 (6)/ 10.3 - 11.6	11.0 ± 0.6 (79)/ 9.7 - 12.5	10.1 ± 0.7 (21)/ 8.9 - 11.4
	POC	6.0 ± 0.1 (10)/ 5.8 - 6.2	6.0 ± 0.2 (30)/ 5.6 - 6.4	6.0 ± 0.2 (17)/ 5.6 - 6.2	6.0 ± 0.2 (6)/ 5.8 - 6.4	5.9 ± 0.2 (79)/ 5.4 - 6.4	6.1 ± 0.2 (21)/ 5.8 - 6.5
	BBC	12.8 ± 0.5 (10)/ 12.1 - 13.8	12.7 ± 0.4 (27)/ 11.8 - 13.2	12.6 ± 0.3 (17)/ 11.9 - 13.2	12.9 ± 0.3 (6)/ 12.5 - 13.3	12.7 ± 0.5 (78)/ 11.3 - 14.0	12.3 ± 0.5 (20)/ 11.6 - 13.4
	ZB	19.0 ± 1.1 (9)/ 16.9 - 20.1	18.7 ± 0.9 (27)/ 17.0 - 20.3	18.8 ± 0.6 (15)/ 18.0 - 20.2	19.2 ± 0.4 (6)/ 18.7 - 19.6	19.8 ± 1.1 (18)/ 17.3 - 22.8	18.3 ± 1.3 (20)/ 16.1 - 20.0
	LM	26.8 ± 1.5 (10)/ 24.2 - 28.9	26.3 ± 1.0 (30)/ 24.5 - 27.8	26.6 ± 1.0 (16)/ 25.1 - 28.4	27.4 ± 1.0 (6)/ 26 - 28.6	27.7 ± 1.4 (78)/ 25.1 - 31.2	25.7 ± 1.3 (21)/ 23.4 - 27.8

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Table 2. Continued..

SEX	CHARACTER	SPECIES					
		M. brevicaudata	*M.* sp. nov. "Trombetas"	*M. touan*	*M.* sp. nov."touan sul"	*M. glirina*	*M. palliolata*
	HMB	3.2 ± 0.3 (10)/ 2.7 - 3.5	3.1 ± 0.2 (31)/ 2.7 - 3.5	3.2 ± 0.2 (16)/ 2.9 - 3.4	3.3 ± 0.2 (6)/ 3.1 - 3.6	3.4 ± 0.2 (79)/ 3.0 - 4.1	3.1 ± 0.2 (21)/ 2.7 - 3.5
	LTR	15.5 ± 0.5 (10)/ 14.9 - 16.4	15.4 ± 0.5 (29)/ 14.5 - 16.1	15.8 ± 0.5 (16)/ 15.2 - 15.8	16.2 ± 0.4 (6)/ 15.4 - 16.6	16.3 ± 0.5 (79)/ 14.9 - 17.6	15.1 ± 0.5 (21)/ 14.2 - 16
	LMS	8.6 ± 0.4 (10)/ 7.8 - 9.0	8.6 ± 0.3 (31)/ 8.0 - 9.1	8.7 ± 0.4 (16)/ 8.2 - 9.3	9.1 ± 0.2 (6)/ 8.8 - 9.4	9.1 ± 0.3 (79)/ 8.0 - 10.2	8.4 ± 0.3 (21)/ 7.8 - 9.0

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Table 3. Results of Student`s t-test between sexes for two species of the *Monodelphis brevicaudata* complex. Only old adult specimens (age classes 7 and 8) were employed (see text for character abbreviations). Sample size (n), Mean, and Standard Deviation (SD) are given for each sex/species. Significant differences (p < 0,05) are represented by an asterisk.

CHARACTER	SPECIES	MALES			FEMALES			p
		n	Mean	SD	n	Mean	SD	
GLS	*M.* sp. nov. "Trombetas"	10	39.202	1.310	12	36.063	0.582	*
	M. glirina	20	41.045	1.462	10	37.433	1.193	*
CBL	*M.* sp. nov. "Trombetas"	9	39.150	1.338	10	36.079	0.488	*
	M. glirina	20	40.854	1.431	10	37.430	1.225	*
RL	*M.* sp. nov. "Trombetas"	9	16.368	0.687	12	14.924	0.416	*
	M. glirina	20	16.799	0.651	9	15.337	0.608	*
NL	*M.* sp. nov. "Trombetas"	9	19.116	0.779	12	17.425	0.656	*
	M. glirina	20	20.228	1.005	9	17.909	0.813	*
PL	*M.* sp. nov. "Trombetas"	10	21.721	0.746	10	19.956	0.348	*
	M. glirina	20	22.769	0.769	10	20.777	0.765	*
MRT	*M.* sp. nov. "Trombetas"	10	15.468	0.437	12	14.678	0.345	*
	M. glirina	20	16.449	0.369	10	15.251	0.318	*
UMS	*M.* sp. nov. "Trombetas"	10	7.800	0.302	12	7.730	0.203	
	M. glirina	20	8.215	0.193	10	7.978	0.102	*
LUI	*M.* sp. nov. "Trombetas"	10	7.800	0.302	12	7.730	0.203	
	M. glirina	20	2.188	0.102	10	2.152	0.085	
LM3	*M.* sp. nov. "Trombetas"	10	2.279	0.129	12	2.334	0.126	
	M. glirina	20	2.466	0.103	10	2.437	0.063	
WM4	*M.* sp. nov. "Trombetas"	10	2.985	0.132	12	2.862	0.171	
	M. glirina	20	3.005	0.115	10	2.896	0.078	
WM3	*M.* sp. nov. "Trombetas"	10	2.681	0.13	12	2.663	0.12	
	M. glirina	20	2.838	0.09	10	2.819	0.102	
HC	*M.* sp. nov. "Trombetas"	10	4.069	0.61	12	3.104	0.215	*
	M. glirina	20	4.720	0.584	10	3.280	0.317	*
PBM3	*M.* sp. nov. "Trombetas"	10	11.930	0.378	12	11.368	0.432	
	M. glirina	20	12.545	0.273	10	12.325	0.333	
PPB	*M.* sp. nov. "Trombetas"	10	3.866	0.247	12	3.896	0.262	
	M. glirina	20	4.190	0.211	10	4.079	0.131	
BFO	*M.* sp. nov. "Trombetas"	10	4.980	0.231	12	4.777	0.345	
	M. glirina	20	4.449	0.29	10	4.195	0.577	
BPG	*M.* sp. nov. "Trombetas"	10	12.388	0.399	12	11.601	0.384	*
	M. glirina	20	12.576	0.476	9	11.873	0.378	*
LTB	*M.* sp. nov. "Trombetas"	9	5.604	0.338	10	5.433	0.212	
	M. glirina	20	5.862	0.206	9	5.721	0.142	
LFI	*M.* sp. nov. "Trombetas"	10	2.741	0.393	10	2.716	0.239	
	M. glirina	19	2.827	0.471	9	2.643	0.278	
BIF	*M.* sp. nov. "Trombetas"	10	0.715	0.08	10	0.706	0.124	
	M. glirina	19	0.683	0.149	10	0.579	0.067	

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Table 3. Continued..

CHARACTER	SPECIES	MALES			FEMALES			p
		n	Mean	SD	n	Mean	SD	
LMP	*M.* sp. nov. "Trombetas"	10	4.615	0.434	9	4.573	0.525	
	M. glirina	17	4.884	0.451	10	4.789	0.72	
BMF	*M.* sp. nov. "Trombetas"	9	0.67	0.099	8	0.726	0.167	
	M. glirina	17	0.584	0.109	10	0.569	0.089	
NB	*M.* sp. nov. "Trombetas"	10	6.237	0.566	12	5.899	0.36	
	M. glirina	20	6.465	0.542	10	5.997	0.269	
BRC	*M.* sp. nov. "Trombetas"	10	6.986	0.488	12	6.076	0.291	*
	M. glirina	20	7.433	0.488	10	6.683	0.34	*
BRO	*M.* sp. nov. "Trombetas"	10	11.815	0.515	12	11.073	0.349	*
	M. glirina	20	12.101	0.549	10	11.475	0.456	
BBC	*M.* sp. nov. "Trombetas"	10	13.847	0.466	11	12.886	0.246	*
	M. glirina	20	13.581	0.508	10	12.825	0.45	*
POC	*M.* sp. nov. "Trombetas"	10	6.192	0.269	12	5.926	0.219	
	M. glirina	20	6.082	0.267	10	6.031	0.142	
ZB	*M.* sp. nov. "Trombetas"	10	21.394	0.932	11	19.232	0.689	*
	M. glirina	20	22.351	1.055	10	20.549	0.907	*
LM	*M.* sp. nov. "Trombetas"	10	29.912	1.063	12	27.144	0.617	*
	M. glirina	20	31.029	1.390	10	28.276	1.015	*
HMB	*M.* sp. nov. "Trombetas"	10	3.610	0.207	12	3.200	0.17	*
	M. glirina	20	3.924	0.271	10	3.666	0.196	
LTR	*M.* sp. nov. "Trombetas"	10	16.502	0.545	12	15.568	0.409	*
	M. glirina	20	17.519	0.387	10	16.229	0.315	*
LMS	*M.* sp. nov. "Trombetas"	10	8.540	0.548	12	8.586	0.225	
	M. glirina	20	9.054	0.177	10	8.855	0.196	

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Table 4. Results of Tukey's multiple comparison tests (post ANOVA test) between pairs of age classes (6 versus 7, and 7 versus 8) for males of three species, and females of two species of the *Monodelphis brevicaudata* complex (see text for character abbreviations). Sample size is showed for each class/sex. M6, M7, and M8 are males of age classes 6, 7 and 8, respectively; F6, F7, and F8 are females of age classes 6, 7 and 8, respectively. Significant differences (p < 0,05) are represented by an asterisk. *M. palliolata* females were not tested and are represented by a "–".

CHARACTER	SPECIES (n)	MALES		FEMALES	
		6 X 7	7 X 8	6 X 7	7 X 8
GLS	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=8, F7=6, F8=9)	*		*	
	M.glirina (M5=12, M6=21, M7=25, M8=27; F5=12, F6=27, F7=16, F8=24)	*	*	*	*
	M.palliolata (M6=10, M7=11, M8=8)	*	*	–	–
CBL	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 14; F6=8, F7=4, F8=9)	*		*	
	M.glirina (M5=12, M6=21, M7=24, M8=26; F5=11, F6=26, F7=16, F8=24)	*	*	*	*
	M.palliolata (M6=10, M7=12, M8 =8)	*	*	–	–
RL	*M*.sp.nov."Trombetas" (M6=7, M7=6, M8= 14; F6=7, F7=6, F8=9)	*			
	M.glirina (M5=10, M6=18, M7=22, M8=26; F5=9, F6=22, F7=15, F8=17)	*	*		
	M.palliolata (M6=7, M7=11, M8 =7)			–	–
NL	*M*.sp.nov."Trombetas" (M6=7, M7=6, M8= 14; F6=7, F7=6, F8=9)				
	M.glirina (M5=10, M6=18, M7=22, M8=26; F5=9, F6=22, F7=15, F8=17)	*	*		*
	M.palliolata (M6=7, M7=11, M8 =7)	*		–	–
PL	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=6, F7=4, F8=10)	*			
	M.glirina (M5=10, M6=19, M7=24, M8=26; F5=11, F6=27, F7=16, F8=23)	*			*
	M.palliolata (M6=10, M7=13, M8 =8)	*	*	–	–
MRT	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)	*			
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*			
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
UMS	*M*.sp.nov."Trombetas" (M6=8, M7=7, M8= 15; F6=9, F7=6, F8=10)		*		
	M.glirina (M5=12, M6=21, M7=24, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
LUI	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=8)				
	M.glirina (M5=12, M6=19, M7=24, M8=26; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=12, M8 =8)			–	–
LM3	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=12, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
WM4	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
WM3	*M*.sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
HC	*M*.sp.nov."Trombetas" (M6=9, M7=7,M8= 15; F6=9, F7=6, F8=10)	*			
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*	*		
	M.palliolata (M6=10, M7=13, M8 =8)	*		–	–

Table 4. Continued..

CHARACTER	SPECIES (n)	MALES		FEMALES	
		6 X 7	7 X 8	6 X 7	7 X 8
PBM3	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*			
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
PPB	*M.*sp.nov."Trombetas" (M6=8, M7=7, M8= 14; F6=9, F7=6, F8=10)				
	M.glirina (M5=11, M6=18, M7=24, M8=28; F5=11, F6=26, F7=15, F8=23)				
	M.palliolata (M6=9, M7=13, M8 =8)			–	–
BFO	*M.*sp.nov."Trombetas" (M6=9, M7=6, M8= 15; F6=8, F7=6, F8=10)				
	M.glirina (M5=13, M6=21, M7=25, M8=27; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=8, M7=12, M8 =8)			–	–
BPG	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)			*	
	M.glirina (M5=13, M6=21, M7=25, M8=28; F5=12, F6=25, F7=16, F8=23)	*	*		
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
LTB	*M.*sp.nov."Trombetas" (M6=8, M7=7, M8= 14; F6=9, F7=4, F8=9)				
	M.glirina (M5=12, M6=21, M7=25, M8=27; F5=11, F6=26, F7=16, F8=23)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
LFI	*M.*sp.nov."Trombetas" (M6=8, M7=6, M8= 13; F6=9, F7=4, F8=10)				
	M.glirina (M5=12, M6=16, M7=24, M8=26; F5=12, F6=23, F7=16, F8=23)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
BIF	*M.*sp.nov."Trombetas" (M6=8, M7=6, M8= 13; F6=9, F7=4, F8=10)				
	M.glirina (M5=12, M6=16, M7=22, M8=26; F5=12, F6=24, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
LMP	*M.*sp.nov."Trombetas" (M6=8, M7=7, M8= 15; F6=9, F7=3, F8=10)				
	M.glirina (M5=13, M6=19, M7=22, M8=26; F5=12, F6=26, F7=16, F8=24)				
	M.palliolata (M6=10, M7=12, M8 =7)			–	–
BMF	*M.*sp.nov."Trombetas" (M6=8, M7=7, M8= 14; F6=9, F7=3, F8=10)				
	M.glirina (M5=13, M6=17, M7=22, M8=27; F5=12, F6=25, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =7)			–	–
NB	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*			
	M.palliolata (M6=10, M7=13, M8 =8)			–	–
BRC	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)	*			
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*	*		
	M.palliolata (M6=10, M7=13, M8 =8)	*	*	–	–
BRO	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=8, F7=6, F8=10)	*			
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*	*	*	
	M.palliolata (M6=10, M7=13, M8 =8)	*		–	–
BBC	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=5, F8=9)	*			
	M.glirina (M5=12, M6=20, M7=25, M8=27; F5=12, F6=27, F7=15, F8=24)	*	*		
	M.palliolata (M6=9, M7=13, M8 =8)		*	–	–
POC	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			–	–

Table 4. Continued..

CHARACTER	SPECIES (n)	MALES		FEMALES	
		6 X 7	7 X 8	6 X 7	7 X 8
ZB	*M.*sp.nov."Trombetas" (M6=8, M7=7, M8= 15; F6=8, F7=6, F8=9)	*			
	M.glirina (M5=12, M6=20, M7=25, M8=28; F5=12, F6=26, F7=16, F8=24)	*	*		*
	M.palliolata (M6=10, M7=12, M8 =8)		*	−	−
LM	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)	*			
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=26, F7=16, F8=24)	*	*	*	
	M.palliolata (M6=10, M7=13, M8 =8)	*	*	−	−
HMB	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)				
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*	*		
	M.palliolata (M6=10, M7=13, M8 =8)		*	−	−
LTR	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=9)	*			
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)	*		*	
	M.palliolata (M6=10, M7=13, M8 =8)			−	−
LMS	*M.*sp.nov."Trombetas" (M6=9, M7=7, M8= 15; F6=9, F7=6, F8=10)		*		
	M.glirina (M5=13, M6=20, M7=25, M8=28; F5=12, F6=27, F7=16, F8=24)				
	M.palliolata (M6=10, M7=13, M8 =8)			−	−

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Table 5. Morphological and geographic comparisons among six species of the *Monodelphis brevicaudata* complex recognized in this study.

CHARACTER	*M. brevicaudata*	*M.* sp. nov. "Trombetas"	*M. touan*	*M.* sp. nov. "touan sul"	*M. glirina*	*M. palliolata*
Middorsal body stripe	brownish or grayish, little or no contrast with laterals	grizzled-gray, contrasting with laterals	grizzled-gray, contrasting with laterals	grizzled-blackish, in sharp contrast with laterals	light grizzled-gray, contrasting with laterals	grizzled-gray, contrasting with laterals
Middorsal rostral stripe	whitish gray or yellowish to orange, narrow (contrasting to undistinguishable)	gray, narrow (commonly ill-defined)	gray, narrow (sometimes ill-defined)	blackish, broad (well-defined)	light gray, broad (well-defined)	gray, broad (well-defined)
Lateral pelage	reddish	reddish	dark reddish	bright dark reddish	light orange	orange
Ventral pelage	cream-gray, contrasting with laterals	grayish cream to yellowish, sharply contrasting with laterals	grayish cream, sharply contrasting with laterals	grayish cream, sharply contrasting with laterals	grayish cream to grayish light-orange, not contrasting with laterals	grayish light-orange to grayish orange, not contrasting with laterals
Throat and chin	distinctly reddish	distinctly reddish	distinctly reddish	distinctly reddish	washed with orange	washed with orange
Body fur extension on tail	unequal on dorsal and ventral sides, up to one fourth of the caudal length dorsally	unequal on dorsal and ventral sides, about one third of the caudal length dorsally	unequal on dorsal and ventral sides, about one third of the caudal length dorsally	unequal on dorsal and ventral sides, up to one fifth of the caudal length dorsally	similar on dorsal and ventral sides, up to one-sixth of the caudal length	similar on dorsal and ventral sides, about one-fifth of the caudal length
Ears, feet, and tail	light brown to dark brown/gray	brown/gray	dark brown/gray	blackish	gray	gray
Interorbital region	narrow	narrow	narrow	narrow	narrow	broad
Zygomatic arches	slightly convergent anteriorly	slightly convergent anteriorly	slightly convergent anteriorly	slightly convergent anteriorly	more rounded anteriorly	sharper convergent anteriorly
Geographic distribution (Figure 8)	Northern Guyana, Venezuela south of the Orinoco river, and northwest of Brazil	Center-South Guyana, Suriname, and Central Brazil north of the Amazon river	French Guiana and Brazil in state of Amapá	Brazilian state of Pará south of the Amazon and east of the Xingu river	Southeastern Peru, northern Bolivia and Brazil south of the Amazon river	Northern Venezuela and northeastern Colombia