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## Molecular phylogeny of short-tailed opossums (Didelphidae: *Monodelphis*): Taxonomic implications and tests of evolutionary hypotheses

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### ABSTRACT

Short-tailed opossums (genus *Monodelphis*) represent one of the most speciose clades of New World marsupials, with 26 currently recognized species that range from eastern Panama to northern Argentina. Here we present the first phylogenetic analyses of the genus based on dense taxonomic sampling and multiple genes. From most sampled species we obtained >4800 bp of DNA sequence from one mitochondrial gene (CYTB), two autosomal exons (IRBP exon 1, BRCA1 exon 11), one autosomal intron (SLC38 intron 7), and one X-linked intron (OGT intron 14). Maximum-parsimony, maximum-likelihood and Bayesian analyses of these data strongly support the monophyly of *Monodelphis* and recover six major clades within the genus. Additionally, our analyses support previous suggestions that several nominal taxa are synonyms of other species (*M. "sorex"* of *M. dimidiata*, *M. "theresa"* of *M. scalops*, *M. "rubida"* and *M. "umbristriata"* of *M. americana*, and *M. "maraxina"* of *M. glirina*). By contrast, four unnamed lineages recovered by our analyses may represent new species. Reconstructions of ancestral states of two discrete characters—dorsal pelage color pattern and habitat—suggest that the most recent common ancestor of *Monodelphis* was uniformly colored (with unpatterned dorsal pelage) and inhabited moist forest. Whereas some dorsal pelage patterns appear to have evolved homoplastically in *Monodelphis*, dorsal stripes may have had a unique historical origin in this genus.

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### 1. Introduction

Short-tailed opossums (*Monodelphis*) comprise one of the most species-rich clades of living New World marsupials. Included species are small terrestrial predators that occur in a wide variety of habitats (lowland rain forest, dry forest, montane forest, and savanna) from eastern Panama to northern Argentina (Pine and Handley, 2008; Solari, 2007; Voss and Jansa, 2009). Formerly an obscure and neglected taxon, *Monodelphis* is now widely known as an important model organism for biomedical research due to the domestication and whole-genome sequencing of *M. domestica*, the grey short-tailed opossum (Keyte and Smith, 2008; Ley, 1987; Mikkelsen et al., 2007; Saunders et al., 1989). Among other

multidisciplinary applications, *M. domestica* has recently been used for studies of neural development (Dooley et al., 2012) gene expression (Das et al., 2012; Sears et al., 2012), and therapeutic oncology (Nair and VandeBerg, 2012). Unfortunately, the ever-increasing popularity of *M. domestica* as a model organism has not been accompanied by systematic understanding of the genus as a whole. *Monodelphis* has never been revised taxonomically, phylogenetic relationships of its member species are incompletely resolved and often weakly supported by existing molecular data, the taxonomic status of several nominal species has been disputed, and other taxa remain undescribed.

The last published taxonomic summary of the genus (Pine and Handley, 2008) recognized 20 species. Subsequently, one species was synonymized with another (Vilela et al., 2010), two nominal taxa previously treated as junior synonyms were recognized as valid species (Pavan et al., 2012; Solari, 2007), and four species were described as new (Pavan et al., 2012; Solari, 2007; Solari et al., 2012; Voss et al., 2012). Altogether, these changes raised

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the total number of recognized species to 25, but Pine et al. (2013) recently recognized a total of 26 species. Unfortunately, many decisions about the validity of nominal taxa currently ranked as species remain untested by analyses of genetic data.

Although the monophyly of *Monodelphis* has been independently supported by numerous studies based on morphological, chromosomal, and/or molecular data (e.g., Caramaschi et al., 2011; Carvalho et al., 2011; Flores, 2009; Hershkovitz, 1992; Jansa and Voss, 2000; Kirsch and Palma, 1995; Lim et al., 2010; Patton and Costa, 2003; Patton et al., 1996; Pavan et al., 2012; Pine et al., 2013; Solari, 2007; Steiner and Catzeflis, 2004; Vilela et al., 2010; Voss and Jansa, 2003; Voss and Jansa, 2009), such studies have included only a few (<50%) of the currently recognized species in the genus. By contrast, the most taxonomically inclusive phylogenetic analysis of *Monodelphis* (Solari, 2010), which was based on partial cytochrome-*b* sequences from 18 species, failed to support generic monophyly. This important study was also the first to recover statistically robust support for species-group relationships within the genus, but key basal relationships were not strongly supported. As pointed out by Solari (2010), sequence data from additional loci, including slowly evolving nuclear genes, coupled with a broader taxonomic sample are needed to further test the monophyly of *Monodelphis* and the relationships among its species.

*Monodelphis* exhibits striking variation in several phenotypic characters, notably pelage coloration (Matschie, 1916; Patton et al., 2000; Pine, 1976; Voss and Jansa, 2009), behavior (diurnality and nocturnality; Emmons and Feer, 1997; Streilein, 1982a), and reproductive strategies (semelparity and iteroparity; Pine et al., 1985; Streilein, 1982b). Of these, only pelage coloration is currently amenable to comparative analysis because behavioral and reproductive traits are unknown for many species. Additionally, pelage coloration has long been of interest to taxonomists because several distinct patterns are easily recognized (Fig. 1), and because these have been used to assign species to species groups (Gilmore, 1941; Matschie, 1916; Miranda-Ribeiro, 1936; Pine, 1976). However, whereas some authors have considered pelage color pattern as indicators of group membership (Gilmore, 1941), others have hypothesized that convergence might be involved (Pine, 1976;

Solari, 2010). Indeed, convergence in pelage traits as a result of adaptation to similar habitats has been demonstrated for other mammals (Dice, 1941; Hoekstra, 2005), and the same might be true for *Monodelphis*.

Herein, we report the results of our analyses of DNA sequence data from one mitochondrial and four nuclear markers, which we obtained from most of the nominal taxa currently recognized as valid species of *Monodelphis* in the literature cited above. Our objectives in this report are (1) to test the monophyly of the genus; (2) to test the genetic integrity of currently recognized species, especially those with noteworthy geographic variation and controversial synonyms; (3) to resolve interspecific relationships within the genus; and (4) to explore the evolution of pelage-color phenotypes in relation to habitat. Biogeographic inferences and phylogeographic analyses, both of which require extensive information about spatial distributions that cannot be effectively summarized here, will be the subject of subsequent publications.

## 2. Materials and methods

### 2.1. Taxon sampling and phylogenetic assumptions

We obtained DNA sequence data from representative material of all currently recognized species of *Monodelphis* except *M. ronaldi* (known only from the holotype; Solari, 2004) and *M. unistriata* (known from just two specimens, both >100 years old; Pine et al., 2013). Additionally, we obtained sequence data from unnamed forms of *Monodelphis* that Pine and Handley (2008) referred to as “species A” (from the Venezuelan llanos) and “species E” (from southeastern Brazil). All of the other three alphabetically designated forms discussed by Pine and Handley (2008)—including “species B” (subsequently named as *M. sanctaerosae* by Voss et al., 2012), “species C” (described as *M. gardneri* by Solari et al., 2012), and “species D” (synonymized with *M. touan* by Pavan et al., 2012)—are also represented by sequence data in this study.

We assessed genetic variation within currently recognized species by including sequence data from as many geographic populations as possible, making a particular effort to obtain multiple

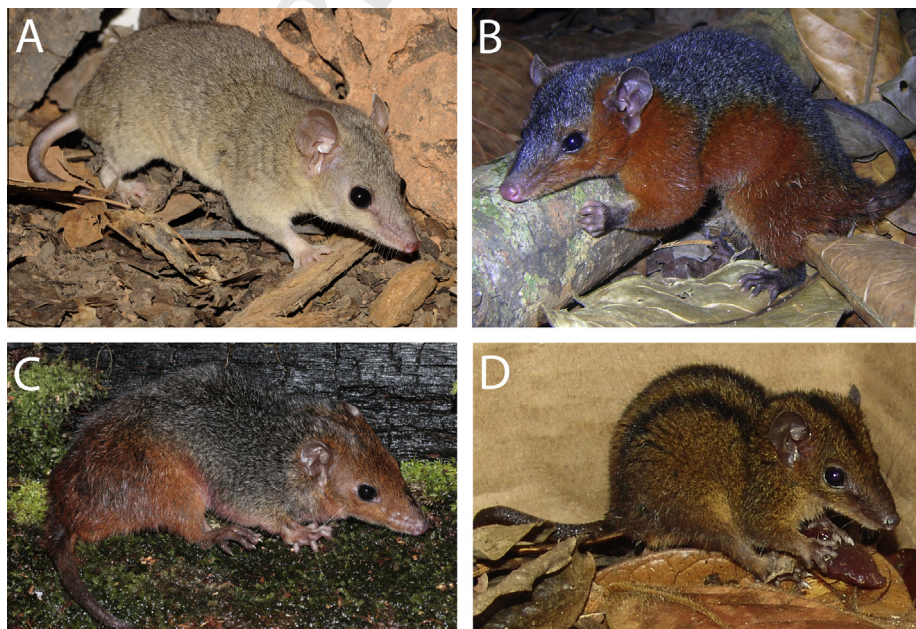


Fig. 1. Species of *Monodelphis* with alternative dorsal pelage color patterns: (A) *M. domestica* (uniform coloration); (B) *M. touan* (reddish sides); (C) *M. emiliae* (reddish head-and-rump); (D) *M. americana* (dorsal stripes). Photo credits (clockwise from top left): T. Semedo, S. Pavan, D. Pavan, T. Semedo.

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