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Morphological, morphometric and genetic variation among cryptic and sympatric species of southeastern South American three-striped opossums (*Monodelphis*: Mammalia: Didelphidae)

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Abstract

Monodelphis is the most diverse genus of the family Didelphidae, whose systematics and taxonomy have not yet been well established. Two of the included species, *Monodelphis americana* and *M. iheringi,* are difficult to distinguish because both present three dorsal black stripes. Furthermore, they show intra- and interspecific variation related to body size and pelage coloration. Because this variation is not well understood, there are problems in correctly identifying these species, which remain poorly collected and thus rare in zoological collections. This study evaluated the morphological and genetic variations in a sample of striped opossums from a single location in southeastern Brazil to understand if the morphological variation observed in individuals from the same location was indicative of the existence of more than one taxon. The comparative analyses of a series from this single locality with museum specimens of other locations revealed variations in the skin and skull qualitative characters that were related to age and sex. Morphological comparisons led to the identification of two morphogroups, which were corroborated by molecular data; the analysis of cytochrome *b* sequences indicated the existence of two clades, with an average divergence of 14%. Thus, the results support the existence of two taxa in the sample, defined as *M. americana* and *M. iheringi.* We confirmed the sympatry of these two species in a location in southeastern Brazil, presented morphological diagnostic characters to distinguish the two species, provided novel phylogenetic information on the group, and also demonstrated the existence of important intra- and interspecific morphological variations related to sexual dimorphism and ontogeny in the group. These results significantly contribute to information on the systematics of the genus.

Key words: age, cytochrome *b*, intrapopulation variation, morphology, sex, syntopy

Resumo em português

Monodelphis é o gênero mais diverso da família Didelphidae, cuja sistemática e taxonomia ainda não se encontram bem estabelecidas. *Monodelphis americana* e *M. iheringi* são de difícil distinção, uma vez que ambos apresentam três listras negras dorsais. Além disso, essas espécies apresentam variação intra e inter-específca relacionada ao tamanho do corpo e à coloração da pelagem. Como esta variação ainda não é bem compreendida, há problemas na correta identificação destas espécies, que ainda são pouco coletadas e, consequentemente, raras em coleções zoológicas. Este trabalho avaliou variações morfológicas e genéticas em uma amostra de catitas de listras de uma única localidade do leste do Brasil, a fim de compreender se as variações morfológicas observadas nos indivíduos em questão eram indicativas da existência de mais de uma espécie na localidade amostrada. A análise comparativa de uma série de indivíduos de uma mesma população, com exemplares de outras espécies e localidades depositados em museus, revelou variação em caracteres qualitativos de crânio e de pelagem, relacionados à idade e ao sexo. As comparações morfológicas levaram à identificação de dois morfogrupos, o que foi corroborado pelos dados moleculares, uma vez que a análise de sequências de citocromo *b* indicou a existência de dois clados, com uma divergência média de 14%. Dessa forma, os resultados deste estudo dão suporte à existência de dois táxons na amostra, definidos como *M. iheringi* e *M. americana*, confirmam a simpatria destas duas espécies em uma nova localidade no sudeste do Brasil, provem caracteres morfológicos diagnósticos capazes de distingui-las, fornecem informações filogenéticas inéditas para o grupo e, ainda, revelam a existência de importantes variações mor-

process, particularly when related to age, still remain obscure (Booth 1990). When generalizing to vertebrates, but with a potential application to *M. americana* as well, Booth (1990) argued that if the synthesis of pigments ceases at a certain age, the posterior growth and allometry may affect the subsequent color pattern because OCCs associated with maturation are controlled by hormones that influence the reproductive phase of individuals. Booth (1990) argued that if the synthesis of pigments ceases at a certain age, the posterior growth and allometry may affect the subsequent color pattern because OCCs associated with maturation are controlled by hormones that influence the reproductive phase of individuals. Booth (1990) also recognized other intraspecific issues because color changes between juveniles and adults can prevent aggression between conspecifics, allowing adults to recognize pre-reproductive members and distinguish them from sexual competitors. The existence of distinct coloration between juveniles that are not reproductively active and adults is favorable to avoid unnecessary energy expenditures and undue copulations.

In general, cryptic species differentiate themselves by non-visual mating signals and/or appear to be under selection that promotes morphological stasis (Bickford *et al.* 2006). Nevertheless ecological conditions (e.g., coexistence, competition for niches, reproduction, similar activity periods and predation avoidance) may sometimes impose morphological stabilizing selection only in specific age/sex classes, diminishing changes in external favorable morphological traits that otherwise would accompany speciation, despite of character displacement imposed by sexual selection; this represents a plausible explanation for the crypsis shown by females and young and subadult males of *M. americana* and adults of both sexes of *M. iheringi*. If morphological changes do not occur concurrently with cladogenesis, and many species are defined by morphological characters, morphological convergence could hamper our comprehension on diversification and speciation processes (Lefébure *et al.* 2006). Consequently, it is reasonably to argue that the number of biological species is most likely greater than the current count of nominal species and that survey lists and the current known geographical distribution of species are also underestimated as well, due solely to crypsis among closely related species.

Taxon sampling. The unusual trap success of striped *Monodelphis* from a single locality in this study can be explained by the use of pitfall traps; these terrestrial three-striped opossums are common but rarely collected without this type of trap (Pardini & Umetsu 2006). In support of this evidence, of the 70 trapped specimens (52 collected and 18 ear-tagged and later released) sampled in this study, 92.85% were captured in pitfalls and 7.15% in live traps. There was a sample-size discrepancy between *M. americana* and *M. iheringi* in the sampling: 65 exemplars of the former and five of the latter were captured.

Monodelphis iheringi is a rare animal (Rossi & Bianconi 2011), with few specimens deposited in mammal collections, which explains the virtual absence of information about this taxon in the literature. Because the amount of traps and time of monthly capture over the year were consistent, we can speculate that there is a peculiarity in the life history of *M. iheringi* that makes it more or less susceptible to the capture by the methods utilized in this study. It is also possible that the populations are naturally maintained in lower relative abundance than those of *M. americana*. In both cases, these results indicate that *M. iheringi* should be further investigated in relation to these aspects.

Finally, we expect that the information contained in this study will significantly contribute to the knowledge on the systematics, morphological and molecular diversity of three-striped short-tailed opossums. Moreover, we emphasize that although extremely important, the morphological traits conventionally used to distinguish *Monodelphis* species are still poorly understood, particularly when considering the scarcity of large series that encompass various sex and age classes in collections. This fact highlights the relevance of molecular analysis to help identify groups for which the taxonomy and systematics are not yet well understood.

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APPENDIX 1.

Gazetteer of collecting localities and examined specimens. Collecting localities are numbered from north to south, and numbers in bold correspond to numbered localities on the map (Fig. 1). States are listed in bold uppercase letters, followed by municipalities in bold, specific localities, latitude and longitude, and elevation (when available). Underlined specimen numbers correspond to those with cytochrome *b* data. For museum acronyms and other abbreviations, see the text.

Monodelphis americana

PERNAMBUCO (PE): Caruaru: **1.** Fazenda Caruaru, 8º22'9"S 36º5'W (MN 24544). SERGIPE (SE): Cristinápolis: **2.** Fazenda Cruzeiro, 13 km SSL de Cristinápolis, 10º29'S 37°46'W (MN 30553–30555). BAHIA (BA): Ilhéus: **3.** Fazenda Santa Maria, 14°42'30.8"S 39°19'W (MN 70051, 70054); **4.** Fazenda Pirataquissé, 14°48'S 39°7'W (MN 11179, 11485, 11492); **5.** Ilhéus, 14°49'S 39°1'60"W (MN 11075, 11483, 11498, 11505, 11524, 20976). ESPÍRITO SANTO (ES): Linhares: **6.** Lagoa Juparanã, 19°19'S 40°5'W (MN 1307); Governador Lindemberg: **7.** Governador Lindemberg, 19°15'10.72"S 40°27'47.23"W (UFES-MAM 932); Santa Teresa: **8.** Reserva Biológica Augusto Ruschi, 19°55'S 40°34'W (MBML 2704, 2710); **9.** Parque Municipal de São Lourenço, 19º55'S 40º37'W (MBML 2869); **10.** Sítio Recanto da Preguiça, 19º57'36"S 40º31'12"W 582m (UFES-MAM 1595); **11.** Estação Biológica de Santa Lúcia, 19º57'54"S 40º32'22"W (UFES-MAM 1599, 1604); Cariacica: **12.** Alto Alegre, Reserva Biológica de Duas Bocas, 20º16'52"S 40º31'19"W 550 m (UFES-MAM 426–33, 502, 503, 504–08, 510, 511, 514, 515, 517–45, *RBDB 49*, *70,73,81,83,85,88–91,95–96,98,101,103–105*); Viana: **13.** Povoação, 20º22'44"S 40º28'31"W (UFES-MAM 829); **14.** Fazenda Boa Baixa, 20º23'20"S 40º27'41"W 28 m (UFES-MAM 757); Castelo: **15.** Parque Estadual do Forno Grande, 20°28'39"S 41°9'58"W (MBML 2553); Guarapari: **16.** Guarapari, 40º30'S 20º40'12"W (MBML 2310, 3023); Anchieta: **17.** Ubu, Samarco, 20°47'13"S 40°34'45"W (MBML 2304); Piúma: **18.** Monte Aghá, 20º50'S 40º41'W (MBML 195). MINAS GERAIS (MG): Caratinga: **19.** Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala, 19º43'S 41º49'W (MBML 2341); Passos: **20.** Passos, 20º43'12"S 46º37'12"W (MN 11728, 20971–74); Além Paraíba: **21.** Fazenda São Geraldo, 21°52'S 42°40'60"W (MN 7568); **22.** Porto Novo, 21°53'12"S 42°42'6"W160m (MN 7312). RIO DE JANEIRO (RJ): Comendador Levy Gasparian: **23.** Fazenda Amazonas, 22°2'30"S 43°11'30"W (MN 43899–43900); Cambuci: **24.** Cambuci, 21°34'S 41°55'W(MN 71941); Sumidouro: **25.** Sumidouro, 22°3'S 42°40'60"W (MN 66070, 66072); Nova Friburgo: **26.** Fazenda Rio Grande, 22°16'12"S 42°31'48"W (MN 68121); Cachoeiras de Macacu: **27.** Subaio, Guapiaçu, Reserva Ecológica do Guapiaçu, 22º27'S 42º46'W (MN 71793, 71816, 71830); Guapimirim: **28.** Estação Ecológica Estadual Paraíso, Centro de Primatologia do Rio de Janeiro, 22°29'18"S 42°54'53"W (MN 71794); Teresópolis: **29.** Fazenda Boa Fé, 22º25'59"S 42º58'59"W (MN 7250); Petrópolis: **30.** Petrópolis, 22º30'36"S 43º10'48"W (MN 10209); Rio de Janeiro: **31.** Santa Teresa, Corcovado, 22°57'S 43°12'40"W (MN 24546); **32.** Tijuca, Trapicheiro, 22°56'11"S 43°14'"W (MN 10305); **33.** Jacarepaguá, Represa Covanca, 22°54'50"S 43°19'60"W (MN 24545); **34.** Parque Estadual Pedra Branca, Colônia Juliano Moreira, 22º56'S 43º24'W (MN 66077); Mangaratiba: **35.** Restinga de Marambaia, 23°4'44"S 43°60'W (MN 1308); **36.** Fazenda Bom Jardim, 22°55'12.1"S 44°6'32.3"W 31m (MN 73745–73750); Ilha Grande: **37.** Praia Vermelha, 23°9'44"S 44°21'W (MN 24400). SÃO PAULO (SP): Paraibuna: **38.** Paraibuna, 23º22'48"S 45º39'W 800m (MN 10988). PARANÁ (PR): Telêmaco Borba: **39.** Fazenda Monte Alegre, 24°12'42"S 50°33'26"W (MN 68215, 68228).

Monodelphis iheringi

ESPÍRITO SANTO (ES): Santa Teresa: **40.** Alto Santo Antônio, Sítio Valsilvestre, 19°52'S 40°31'W (MBML 2131); **9.** Parque Municipal de São Lourenço, 19º55'S 40º37'W (MBML 2346); Cariacica: **12.** Alto Alegre, Reserva Biológica de Duas Bocas, 20º16'52"S 40º31'19"W 550m (UFES-MAM 509, 512–513, 516, *RBDB 86*). RIO DE JANEIRO (RJ): Santa Maria Madalena: **41.** Parque Estadual do Desengano, 22º0'S 42º0'W (MN 71935); Cachoeiras de Macacu: **42.** Parque Estadual dos Três Picos, 22 27'S 42 39'W (MN 71947); 27. Subaio, Guapiaçu, Reserva Ecológica do Guapiaçu, 22º27'S 42º46'W (MN 71814, 71795); Parati: **43.** Pedra Branca, 23°13'S 44°43'W (MN 6221, 8203). SÃO PAULO (SP): Ubatuba: **44.** Parque Estadual da Serra do Mar, Núcleo Picinguaba, Casa da Farinha, 23°20'S 44°50'W (MN 69875). Unknown locality: (MN 73751).

Monodelphis scalops

ESPÍRITO SANTO (ES): Santa Teresa: Reserva Biológica Augusto Ruschi, 19º55'S 40º34'W (MBML 326); Santa Teresa, 19º55'S40º36'W (MBML 59, 102). MINAS GERAIS (MG): Simonésia: Reserva Particular do Patrimônio Natural Estação Biológica da Mata do Sossego, 20°4'19"S 42°4'10"W (UFMG 2251).