LAURA RODRIGUES VIEIRA DE ALENCAR

**Ecomorfologia em serpentes neotropicais: um estudo de
caso com a tribo Pseudoboini**

**Ecomorphology in Neotropical snakes: a study with the
tribe Pseudoboini**

São Paulo
2010

LAURA RODRIGUES VIEIRA DE ALENCAR

**Ecomorfologia em serpentes neotropicais: um estudo de
caso com a tribo Pseudoboini**

**Ecomorphology in Neotropical snakes: a study with the
tribe Pseudoboini**

Dissertação apresentada ao Instituto de
Biociências da Universidade de São Paulo,
para a obtenção de Título de Mestre em
Ciências, na Área de Ecologia.

Orientador(a): Marcio Roberto Costa Martins

São Paulo
2010

Ficha Catalográfica

Alencar, Laura

Ecomorfologia em serpentes
neotropicais: um estudo de caso com a tribo
Pseudoboini.

86 páginas

Dissertação (Mestrado) - Instituto de
Biociências da Universidade de São Paulo.
Departamento de Ecologia.

1. Evolução 2. Serpentes 3. Ecologia
I. Universidade de São Paulo. Instituto de
Biociências. Departamento de Ecologia.

Comissão Julgadora:

Prof(a). Dr(a). Marcio Roberto Costa Martins
Universidade de São Paulo
Orientador

Dedico este trabalho à Coleção Herpetológica
“Alphonse Richard Hoge” do Instituto Butantan
e aos amigos queridos que fiz por lá.

Agradecimentos

Ao Marcio Martins pela orientação, amizade e por me dar a oportunidade de tentar desvendar a tribo Pseudoboini.

À Marília Gaiarsa pela amizade e ajuda indispensável na realização deste trabalho. Má, este trabalho também é seu!

À Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (processo nº 2007/56921-6) pelo apoio financeiro.

Ao Ricardo J. Sawaya e Ronaldo Fernandes por aceitarem fazer parte da banca contribuindo assim para a melhoria deste trabalho.

Ao Hussam Zaher e Felipe Grazziotin pelas valiosas informações acerca da taxonomia das espécies e por nos cederem a filogenia da tribo Pseudoboini, sem a qual a realização desta dissertação seria impossível.

Agradeço ao Danilo Guarda e Rodrigo Scartozzoni pela ajuda com as análises estatísticas.

À Paula Valdujo, agradeço pela enorme ajuda e discussões essenciais durante o desenvolvimento deste trabalho.

Ao Valdir J. Germano pela amizade querida, paciência de Jó, apoio e ajuda constante na coleção do Instituto Butantan, e por dividir comigo seu grande conhecimento sobre serpentes.

Ao Paulo “Miúdo” Guimarães, André Eterovic e Luís Schiesari pelas críticas e sugestões feitas à versão preliminar do trabalho.

Ao Hebert Ferrarezzi, Otávio A. V. Marques e Ricardo J. Sawaya pelas críticas e sugestões feitas ao longo do desenvolvimento deste trabalho.

Ao Francisco L. Franco “Kiko” por permitir o acesso à coleção de serpentes do Instituto Butantan.

À Ana L. Prudente por permitir o acesso à coleção herpetológica do Museu Paranaense Emílio Goeldi e pelo carinho e hospitalidade com que nos recebeu em Belém. Agradeço também aos alunos da herpetologia do MPEG por toda ajuda durante a estadia e trabalho de laboratório.

Ao Marcos A. de Carvalho por permitir o acesso à coleção herpetológica da Universidade Federal do Mato Grosso.

Ao Júlio C. Moura-Leite por permitir o acesso à coleção herpetológica do Museu de História Natural Capão da Imbuía.

Ao Hussam Zaher por permitir o acesso à coleção herpetológica do Museu de Zoologia da Universidade de São Paulo.

Ao Guarino Coli por permitir o acesso à coleção herpetológica da Universidade de Brasília.

Ao Taran Grant por permitir o acesso à coleção herpetológica da Pontifícia Universidade Católica do Rio Grande do Sul e à Glaucia Pontes pela ajuda no trabalho de laboratório.

Agradeço imensamente a todos que contribuíram com informações sobre os Pseudoboini. Tais informações foram extremamente importantes e necessárias para a realização deste trabalho: Renato S. Bérnils, Paulo S. Bernarde, Christina Strüssmann, Marco Sena, Mauro Teixeira Jr., Paula H. Valdujo, Renato Recoder, Agustín Camacho, Antônio S. Argôlo, Otávio A. V. Marques, Ricardo J. Sawaya, Cristiano Nogueira, Gleomar Maschio, Ricardo Kawashita Ribeiro, Ana Prudente, Murilo Guimarães, Rodrigo Scartozzoni, Fausto E. Barbo, Renata Orofino, Thiago Santos, Sérgio A. Morato, Teresa C. S. Ávila Pires, Marinus Hoogmoed, Laurie J. Vitt, Marcos A. de Carvalho, Ângelo Dourado, João C. Costa, Fabrício Sarmiento, Fernanda Stender e Eros J. Sanches.

Aos amigos do Laboratório de Herpetologia, Laboratório de Ecologia e Evolução e Laboratório de Artrópodes do Instituto Butantan: Daniela Gennari “Dani”, José Pedro Marinho “Pará”, Valdir J. Germano “Val”, Francisco L. Franco “Kiko”, Marcelo Duarte, Paulo Passos, João Paulo Bresciani, Jorge N. Rosa, Paulo Machado, Alexandre “Xandão” Missassi, Fernando Julio “Fernandão”, Cláudia Parisoto, Angélica Tesser, Mariza de Lima, Fátima Aparecida Cagnotto, Antônio “Garotinho” Carlos Barbosa, Regina Elaine da Silva, Sandra Ferrao, Letícia Sueiro “Lê”, Thais “Caatinga” Guedes, Fernanda Centeno, Thaís Condez, Murilo Guimarães “Mu”, Cristian Gomes, Verônica Barros, Amom Mendes, Sérgio Serrano “Coy”, Fausto E. Barbo, Greyce Camargo, Rodrigo Scartozzoni, Danilo Guarda “Itu”, Gustavo Perroni “Tulipa”, Andria de Paula “Paroa”, Vanessa Penna e André “Jaú” Marsola Giroti. Obrigada a todos vocês por tornarem esses dois anos e meio simplesmente maravilhosos!

Aos amigos e colegas do Laboratório de Ecologia, Evolução e Conservação de Vertebrados “Labvert”: Marília P. Gaiarsa “Má”, Hamanda Cavalheri, Irina Barros, Paula H. Valdujo e Victor Vettorazzo. Agradeço a vocês pela amizade, ajuda, companheirismo e ótimo convívio ao longo desses anos.

Aos queridos amigos da Universidade de São Paulo, Ana Mengardo, Gustavo Oliveira e Jomar Barbosa. Obrigada por tornarem minhas idas à USP sempre divertidas, pela amizade que conquistamos, pelas conversas (e mais conversas) e por estarem (quase) sempre dispostos a tomar uma cervejinha para desestressar. Agradeço também a secretária da pós-graduação Dalva Molnár por estar sempre à disposição para sanar dúvidas e tentar nos acalmar em momentos de (quase) desespero.

À sempre animada Gabriela Cortez “Gabi”, agradeço pela amizade e por nunca deixar que qualquer “tempo ruim” se aproximasse.

Agradeço à minha família querida: meu pai Francisco V. Alencar, minha mãe Claudia R. V. Alencar e meus irmãos Ana e Joaquim Alencar pelo apoio constante e indispensável, por agüentarem a distância e por tentarem entender esta paixão esquisita por serpentes. Dedico essa dissertação também a vocês.

Índice

Introdução Geral	09
<i>Objetivos</i>	11
<i>Literatura Citada</i>	11
Capítulo 1. Evolutionary morphological relationships of snakes to different diets: are the expected changes always evident?.....	15
<i>Abstract</i>	16
<i>Introduction</i>	17
<i>Material and Methods</i>	18
<i>Results</i>	21
<i>Discussion</i>	23
<i>Literature Cited</i>	27
<i>Tables and Figures</i>	32
Capítulo 2. Morphological adaptations to arboreality in snakes: a case study with a Neotropical lineage.....	38
<i>Abstract</i>	39
<i>Introduction</i>	40
<i>Material and Methods</i>	41
<i>Results</i>	43
<i>Discussion</i>	45
<i>Literature Cited</i>	48
<i>Tables and Figures</i>	52
Conclusão Geral	64
Resumo Geral	66
General Abstract	68
Apêndices/Appendices	70

Introdução Geral

As serpentes representam uma das mais notáveis radiações adaptativas ocorridas durante a história evolutiva dos vertebrados. O sucesso desta radiação pode ser visualizado através do número de espécies existentes e suas distribuições em várias partes do planeta (Lillywhite e Henderson, 1993). As serpentes constituem uma linhagem bastante variada quanto à morfologia (e. g., forma do corpo, tamanho da cabeça, comprimento da cauda) e em termos de especializações em sua ecologia. Tais especializações incluem diferenças na biologia alimentar e no uso de ambientes. Estes fatores são considerados como alguns dos determinantes da amplitude de habitats ocupados, bem como do sucesso do grupo durante sua história evolutiva (Greene, 1997; Alveiro-Lins et al., 2006).

A origem, a manutenção e a diversificação da forma e função de um organismo têm sido atribuídas principalmente à adaptação ao ambiente externo através da seleção natural (Vincent et al., 2006). Dessa forma, variações morfológicas observadas nas serpentes refletiriam o uso de diferentes recursos, como o consumo de diferentes tipos e tamanhos de presa (Pough e Groves, 1983; Savitzky, 1983; Martins et al., 2002; Teixeira e Bennemann, 2007) ou o uso de diferentes substratos (Lillywhite e Henderson, 1993; Greene, 1997).

Possíveis associações entre a dieta e a morfologia em serpentes têm sido apontadas na literatura (Savitzky, 1983; Martins et al., 2002; Vincent et al., 2006). Por exemplo, Martins et al. (2002), estudando espécies do gênero *Bothrops*, apontaram uma possível associação entre o aumento de mamíferos na dieta e um aumento da robustez nestas serpentes. O modo como o animal utiliza os microhabitats disponíveis e suas implicações físicas também podem influenciar a evolução da forma do corpo em serpentes (Miles e Ricklefs, 1984; Cadle e Greene, 1993; Martins et al., 2001; Pizzatto et al., 2007b). Diversas são as síndromes morfológicas comumente associadas ao uso do ambiente por serpentes. Espécies que apresentam hábitos predominantemente arborícolas tendem a apresentar corpo mais delgado, comprimido lateralmente e caudas mais longas quando comparadas às espécies que utilizam outros microhabitats. Já as serpentes de hábitos terrestres tendem a apresentar morfologia generalizada (Cadle e Greene, 1993; Lillywhite e Henderson, 1993; Greene, 1997; Martins et al., 2001; Pizzatto et al., 2007a, b). Entretanto, a forma do corpo em serpentes muitas vezes pode ser conservativa, ou seja, ser resultado de forte inércia filogenética (Vitt e Valgilder, 1983; Pizzatto et al., 2007b).

A diversidade de espécies de serpentes neotropicais é enorme e as mudanças morfológicas associadas aos seus hábitos alimentares e uso do ambiente ainda são pouco conhecidas (Cadle e Greene, 1993; Pizzatto, 2005). Estudar tais mudanças em grupos monofiléticos de serpentes permite que estas relações sejam avaliadas sob um contexto evolutivo (Martins et al., 2001; Pizzatto et al., 2007a, b).

A subfamília Xenodontinae, atualmente alocada na família Dipsadidae (Zaher et al., 2009), é composta por cerca de 90 gêneros e mais de 500 espécies, todas restritas ao Novo Mundo (Cadle e Greene, 1993; Vidal et al., 2010). Esta subfamília é caracterizada por uma grande diversidade morfológica e ecológica (Cadle e Greene, 1993; Vidal et al., 2000). Várias tribos têm sido propostas para os Xenodontinae, sendo que pelo menos três delas são aparentemente monofiléticas: Hydropsini, Xenodontini e Pseudoboini (Vidal et al., 2000; Zaher et al., 2009; Vidal et al., 2010).

A tribo Pseudoboini atualmente compreende nove gêneros, cerca de 47 espécies e apresenta ampla distribuição, ocorrendo desde o México até a Argentina (Uetz, 2007). Segundo Pizzatto e Marques (2002), a tribo abrange serpentes consideradas, em geral, de tamanho médio. Entretanto *Clelia clelia* e *Clelia plumbea* podem atingir 2,5 m de comprimento total (Scott et al., 2006). Em relação aos hábitos alimentares, as informações existentes sugerem que serpentes da tribo Pseudoboini se alimentam principalmente de lagartos e pequenos mamíferos, com algumas espécies mais especializadas em lagartos (Andrade e Silvano, 1996; Martins e Oliveira, 1998; Prudente et al., 1998; Marques et al., 2001). A ingestão de ovos foi ocasionalmente registrada em várias espécies da tribo (Cunha e Nascimento, 1983; Vitt e Vangilder, 1983). Entretanto, *Drepanoides anomalus* parece possuir uma dieta especializada em ovos de lagartos (e.g. Martins e Oliveira, 1998). Além disso, a ofiofagia, seja ela preferencial ou não, foi também registrada em várias espécies da tribo (e.g. Prudente et al., 1998; Pinto e Lema, 2002).

Com relação ao uso do ambiente, as espécies desta tribo parecem ser predominantemente terrestres (e. g., *Clelia* spp., *Boiruna* spp., *Mussurana* spp., *Pseudoboa* spp.), porém algumas também podem ser consideradas semi-arborícolas (e. g., *Drepanoides anomalus*, *Siphlophis cervinus*, *Siphlophis compressus*) e semi-fossoriais (*Phimophis* spp.) (Cunha e Nascimento, 1978; Cunha e Nascimento, 1983; Martins e Oliveira, 1998; Marques et al., 2001).

As espécies da tribo Pseudoboini aparentemente apresentam relativa diversidade quanto à morfologia, dieta e uso de ambiente. Devido a esta grande variação em hábitos, este grupo parece ser objeto de estudo interessante para trabalhos em ecologia comparativa. Estes

estudos, utilizando filogenias disponíveis para as linhagens de interesse, permitem a exploração de possíveis relações entre mudanças de hábitos e mudanças na morfologia (ver Martins, 2000), bem como, a reconstrução dos fenótipos durante a história evolutiva do grupo. No caso das serpentes neotropicais, alguns estudos deste tipo já foram realizados com viperídeos (e.g. Martins et al., 2001; Martins et al., 2002), bóideos (Pizzatto et al, 2007*a, b*) e com várias linhagens nas quais ocorrem espécies aquáticas (Scartozzoni, 2005).

Objetivos

O objetivo geral deste trabalho é explorar as mudanças em ecologia e morfologia sofridas pelas serpentes da tribo Pseudoboini durante sua história evolutiva e os fatores que poderiam estar relacionados com tais mudanças. A dissertação divide-se em dois capítulos apresentados sob o formato de artigo nos moldes da revista *Herpetologica*. O capítulo 1 tem por objetivos principais analisar a dieta, bem como as possíveis relações entre esta e aspectos morfológicos, além de explorar como a dieta e a morfologia possivelmente relacionada evoluíram dentro da tribo. O capítulo 2 trata das possíveis relações entre o uso do ambiente arborícola e a morfologia, e da evolução destes durante a história evolutiva das serpentes da tribo Pseudoboini. Ao final da dissertação é apresentada uma conclusão geral, abordando e discutindo os principais resultados do trabalho.

Literatura citada

- ALVEIRO-LINS, G., O. ROCHA-BARBOSA, M. G. SALOMÃO, G. PUERTO, AND M. F. C. LOGUERCIO. 2006. Topographical Anatomy of the Blunthead Treesnake, *Imantodes cenchoa* (Linnaeus, 1758) (Colubridae: Xenodontinae). *Internacional Journal of Morphology* 24:43-48.
- ANDRADE, R. O., AND R. A. SILVANO. 1996. Comportamento alimentar e dieta da falsa-coral *Oxyrhopus guibei* (Serpentes, Colubridae). *Revista Brasileira de Zoologia* 13:143-150.
- CADLE, J. E., AND H. W. GREENE. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281-293. *In* R. E. Ricklefs, and D. Schluter (Eds.), *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, USA.

- CUNHA, O. R., AND F. P. NASCIMENTO. 1978. Ofídios da Amazônia X. As cobras da região leste do Pará, Belém. Museu Paranaense Emílio Goeldi Publicações Avulsas 31:1-218.
- CUNHA, O. R., AND F. P. NASCIMENTO. 1983. Ofídios da Amazônia XIX. As espécies de *Oxyrhopus* Wagler, com uma subespécie nova, e *Pseudoboa* Schneider, na Amazônia Oriental e Maranhão (Ophidia: Colubridae). Boletim do Museu Paranaense Emílio Goeldi 1:1-42.
- GREENE, H. W. 1997. Snakes: the evolution of mystery in nature. The University of California Press, Berkley, California, USA.
- LILLYWHITE, H. B., AND R. W. HENDERSON. 1993. Behavioral and functional ecology of arboreal snakes. Pp. 1-48. In R. A. Seigel, and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York, USA.
- MARTINS, E. 2000. Adaptation and the comparative method. Trends in Ecology and Evolution 15:296-299.
- MARTINS, M., AND E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150.
- MARTINS, M., M. S. ARAÚJO, R. J. SAWAYA, AND R. NUNES. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). Journal of Zoology 254:529-538.
- MARTINS, M., O. A. V. MARQUES, AND I. SAZIMA. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. Pp. 307-328. In G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- MARQUES, O. A. V., A. ETEROVIC, AND I. SAZIMA. 2001. Serpentes da Mata Atlântica: guia ilustrado para a Serra do Mar. Holos Editora, Ribeirão Preto, São Paulo, Brazil.
- MILES, D. B., AND R. E. RICKLEFS. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. Ecology 65:1629-1640.
- PINTO, C., AND T. LEMA. 2002. Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). Iheringia 92:9-19.
- PIZZATTO, L. 2005. Body size, reproductive biology and abundance of the rare Pseudoboine snakes, genus *Clelia* and *Boiruna* (Serpentes: Colubridae) in Brazil. Phyllomedusa 4:111-122.
- PIZZATTO, L., AND O. A. V. MARQUES. 2002. Reproductive biology of the false coral *Oxyrhopus guibei* (Colubridae) from Southeastern Brazil. Amphibia-Reptilia 23:495-504.

- PIZZATTO, L., S. M. ALMEIDA-SANTOS, AND R. SHINE. 2007a. Life history adaptations to arboreality in snakes. *Ecology* 88:359-366.
- PIZZATTO, L., O. A. V. MARQUES, AND M. MARTINS. 2007b. Ecomorphology of boine snakes, with emphasis on South American forms. Pp. 254-269. *In* R. W. Henderson (Org.), *Biology of Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- POUGH, F. H., AND J. D. GROVES. 1983. Specializations of the body form and food habits of snakes. *American Zoologist* 23:443-454.
- PRUDENTE, A. L. C., J. C. MOURA-LEITE, AND S. A. A. MORATO. 1998. Alimentação das espécies de *Siphlophis* Fitzinger (Serpentes, Colubridae, Xenodontinae, Pseudoboini). *Revista Brasileira de Zoologia* 15:375-383.
- SAVITZKY, A. 1983. Coadapted character complexes among snakes: fossoriality, piscivory and durophagy. *American Zoologist* 23:397-409.
- SCARTOZZONI, R. R. 2005. Morfologia de serpentes aquáticas neotropicais: um estudo comparativo. M.s.c. Dissertation, Universidade de São Paulo, São Paulo, São Paulo, Brazil.
- SCOTT, N. J., JR., A. R. GIRAUDO, G. SCROCCHI, A. L. AQUINO, P. CACCIALI, AND M. MOTTE. 2006. The Genera *Boiruna* and *Clelia* (Serpentes: Pseudoboini) in Paraguay and Argentina. *Papéis Avulsos de Zoologia* 46:77-105.
- TEIXEIRA, I., AND S. T. BENNEMANN. 2007. Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. *Biota Neotropica* 7:67-76.
- UETZ, P. 2007. The new reptile database. Available at [HTTP://www.reptile-database.org](http://www.reptile-database.org). Zoological Museum Hamburg, Hamburg, Hamburg, Germany.
- VIDAL, N., S. G. KINDL, A. WONG, AND S. B. HEDGES. 2000. Phylogenetic relationships of Xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. *Molecular Phylogenetics and Evolution* 14:389-402.
- VIDAL, N., M. DEWYNTER, AND D. J. GOWER. 2010. Dissecting the major American snake radiation: A molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies* 333:48-55.
- VINCENT, S. E., P. D. DANG, A. HERREL, AND N. J. KLEY. 2006. Morphological integration and adaptation in the snake feeding system: a comparative phylogenetic study. *Journal of Evolutionary Biology* 19:1545-1554.
- VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* 4:273-296.
- ZAHER, H., F. G. GRAZZIOTIN, J. E. CADLE, R. W. MURPHY, J. C. MOURA-LEITE, AND S. L. BONATTO. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with

emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia* 49:115-153.

Capítulo 1

EVOLUTIONARY MORPHOLOGICAL RELATIONSHIPS OF SNAKES TO DIFFERENT DIETS: ARE THE EXPECTED CHANGES ALWAYS EVIDENT?

LAURA R. V. ALENCAR^{1,3}, MARÍLIA P. GAIARSA¹, HUSSAM ZAHER², FELIPE GRAZZIOTIN², AND
MARCIO MARTINS¹

¹*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do
Matão, Travessa 14, Cidade Universitária, São Paulo, SP, Brasil, CEP 05508-090*

²*Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brasil, CP 42.494, 04218-
970*

³ CORRESPONDENCE: laura.alencar@globo.com

ABSTRACT: Snakes of the tribe Pseudoboini occur from Mexico to Argentina and comprise about 47 species. Based on scattered information in the literature, the pseudoboines show relatively high diet diversity, with some apparent cases of diet specialization. Here we use this tribe to explore hypotheses of possible adaptative relationships of diet in relation to morphology and microhabitat use. We also explore how morphological and ecological characters evolved in this snake lineage. Using published and unpublished data, we provide a comprehensive description of diet variation in the tribe and specifically address the questions: (1) an increase in the proportion of relatively large prey (small mammals) in diet would be associated to an increase in robustness and head size? (2) an increase in the use of vegetation would be associated with a decrease in the consumption of large prey like small mammals? The diet of pseudoboine snakes is composed mainly by lizards and small mammals. Of the 22 species for which a minimum number of prey records was obtained, nine are diet generalists, six are lizard specialists, three are small mammal specialists, two are snake specialists, one is a lizard egg specialist, and one is a bird egg specialist. The increase in the consumption of small mammals seems not to be associated with the evolution of a more robust body or a larger head. We failed to find a relationship between diet and microhabitat use. The reconstruction of diet on the phylogeny of the tribe indicates that lizard, small mammals and snake specializations occurred independently in terminal taxa, at least twice. Diet specialization in bird eggs seems to be an autapomorphy of *Rhachidelus brazili* and a specialization in lizard eggs is probably an autapomorphy of *Drepanoides anomalus*. Along the diversification of the tribe, robustness seemed to have decreased in the ancestor of the genus *Siphlophis*, and increased substantially in *Rhachidelus brazili*. Head size decreased in the ancestor of the genus *Siphlophis* and in *Oxyrhopus petola*, and increased substantially in *Phimophis guianensis*, in the ancestor of *Oxyrhopus trigeminus* and *O. rhombifer* and in *Rhachidelus brazili*. Pseudoboine snakes are highly diversified in their feeding habits, and many types of specialization appeared during the evolutionary history of the group. Our results show that pseudoboines are highly diversified in their feeding habits, and that many types of specialization appeared during the evolutionary history of the group. Phylogenetic inertia, an ancestor with a robustness and a head size adequate to allow a diet based on small mammals, as well as the action of other selective agents could have exerted a strong influence in the evolution of morphological aspects in pseudoboine snakes. Additionally, Pseudoboine snakes do not seem to be an ideal group to test the hypothesis concerning the relationship between diet and microhabitat.

Key Words: Ecology; Ecomorphology; Evolution; Pseudoboini;

ADAPTATIONS to different diets are an obvious aspect of the evolutionary diversification of animals (Queiroz and Rodriguez-Robles, 2006). Snakes are highly diversified in their diet and morphology, and evidence of adaptive relationships between these two biological aspects has repeatedly been reported (Savitzky, 1983; Martins et al., 2002; Vincent et al., 2006). These relationships are usually attributed to environmental selective agents, which select the organisms according to resource use (Pianka, 2000; Teixeira and Bennemann, 2007). Therefore, morphological variations observed in snakes would reflect the different uses of resources, like the consumption of different kinds and sizes of prey (Pough and Groves, 1983; Savitzky, 1983; Martins et al., 2002; Teixeira and Bennemann, 2007). For example, the width of preys ingested by snakes is limited by the elongate, narrow body typical of this group. Thus, an increase in the consumption of larger prey (like small mammals) would likely be associated with an increase in body circumference and, consequently, an increase in robustness; this trend is evident, for instance, in some vipers (Martins et al., 2002). Likewise, the size (especially the width) of prey ingested by a snake is limited by its gape (e. g., Greene, 1983). Therefore, an increase in the consumption of larger prey would be associated with an increase in gape (and, thus, the size of the head; Shine, 1991).

The use of different microhabitats can also influence the diet of snakes. The effect of physical limitations imposed by the environment on morphology and prey availability in each kind of microhabitat are some of the possible causes of diet differences among species which use different microhabitats (Savitzky, 1983; Lillywhite and Henderson, 1993; Martins et al., 2002). For instance, among snakes of the genus *Bothrops*, mammal specialization does not occur in semi-arboreal species, which have a slender body compared to species that use other microhabitats (Martins et al., 2002).

The development of comparative methods (see Brooks and McLennan, 1991; Harvey and Pagel, 1991; Martins and Hansen, 1996) allowed the evaluation of hypotheses about phenotypic evolution; it became possible, for example, to explore possible relationships between changes in habits and morphology, using the phylogenies available for the lineages of interest (Klingenberg and Ekau, 1996; Barbosa and Moreno, 1999; Kohlsdorf et al., 2001; Lindeman, 2008). For Neotropical snakes, studies of this kind have been made with vipers (Martins et al., 2001; Martins et al., 2002; Araújo and Martins, 2006) and boine snakes (Pizzatto et al., 2007a, b). Indeed, comparative analyses exploring changes in feeding habits that occurred during the evolutionary history of snakes, were done only for the genus *Bothrops* (Martins et al., 2002), for some species that are lizards or bird egg specialists

(Queiroz and Rodriguez-Robles, 2006) and for species of the sub-family Natricinae (Vincent et al., 2009).

Diet and morphology of pseudoboine snakes are widely diversified, making this tribe an interesting subject for studies concerning adaptative relationships between these traits, and thus for comparative studies. The tribe belongs to the family Dipsadidae, sub-family Xenodontinae and has been considered as a monophyletic group by several authors (e. g., Vidal et al., 2000; Zaher et al., 2009; Vidal et al., 2010). The tribe comprises nine genera and about 47 species, occurring from México to Argentina (Uetz, 2007).

According to Pizzatto and Marques (2002), pseudoboines are, in general, moderate-sized snakes; most species seem to be terrestrial (e. g., *Clelia* spp., *Boiruna* spp., *Mussurana* spp., *Pseudoboa* spp.), but some are considered semi-arboreal (e. g., *Drepanoides anomalus*, *Siphlophis* spp.) and semi-fossorial (e.g., *Phimophis* spp.) (Cunha and Nascimento, 1978, 1983; Martins and Oliveira, 1998; Marques et al., 2001; Marques et al., 2005; Bernarde and Abe, 2006).

Scattered information concerning feeding habits of pseudoboines (e.g., Andrade and Silvano, 1996; Martins and Oliveira, 1998; Prudente et al., 1998) indicates that most species eat mainly lizards and small mammals, with some more specialized in lizards. Oophagy and ophiophagy were occasionally recorded for some species of the tribe (see Vitt and Vangilder, 1983; Prudente et al., 1998; Pinto and Lema, 2002) and *Drepanoides anomalus* was considered a specialist in lizard eggs (Martins and Oliveira, 1998).

Here we use the tribe Pseudoboini to explore hypotheses of possible adaptative relationships of diet in relation to morphology and microhabitat use. We also explore how morphological and ecological characters evolved in this snake lineage. Using published and unpublished data, we provide a comprehensive description of diet variation in the tribe and specifically address the questions: (1) an increase in the proportion of relatively large prey (small mammals) in diet would be associated to an increase in robustness and head size? (2) an increase in the use of vegetation would lead to a decrease in the consumption of large prey like small mammals?

MATERIALS AND METHODS

Ecological data

We analyzed the diet of 33 species of pseudoboines by examining the digestive tracts of 871 preserved specimens (Appendix I) and by gathering literature data and observations granted by other researchers (Appendix II). Whenever possible, samples consisted of a similar

proportion of juveniles and adults. A species was considered a diet specialist when a single type of prey represented at least 70% of all prey items; otherwise it was considered a generalist. Although arbitrary, this percentage is similar to those used in studies concerning the diversity of snakes feeding habits (e.g., Martins et al., 2002) and seems to properly categorize the species in relation to their degree of feeding specialization. This categorization and the calculation of the proportion of small mammals in diet (see *Analyses*; Table 1) were made only for those species for which at least eight prey records were available; we think that less than eight individual prey may not be enough for characterizing the diet of a given species.

Information on microhabitat use was obtained by gathering literature data, data from scientific collections, and observations granted by other researchers (Appendix III). Only the data obtained for snakes that were active during the observations were included in the microhabitat analysis. We used only species for which at least eight observations of microhabitat were available, using the same rationale used for the number of individual prey to characterize diet. Here, microhabitat data are used as a proportion of microhabitat use (proportion of individuals found on vegetation; Martins et al. 2001; Table 1). Species in which the proportion of vegetation use was equal or greater than 0.15 were considered semi-arboreal. Although arbitrary, this distinction decreases the chance of considering a species as semi-arboreal when it only rarely uses the vegetation (Martins et al., 2001).

Morphological data

We measured body circumference (BC) and head length (HL), width (HW), and height (HH) of preserved adult male specimens by using a measuring tape (1 mm) and a dial caliper (0.1 mm). Specimens that had prey items in the stomach were not measured. Body circumference was used for estimates of robustness and head measurements were used to calculate head volume (HV) through the formula of half of an ellipsoid: $V_{cab} = (4/3 \times \pi \times 1/2HW \times 1/2HH \times HL)/2$. In the following analysis, we used the ratio between these variables and the snout-vent length (RBC and RHV; see García-Berthou, 2001).

Whenever possible, these measurements were obtained from 20 adult males of each species. However, some species are rare in collections. Thus, only the species for which at least five individuals could be measured were included (Table 1).

Analyses

In the following analyses, we used the average ratio obtained for the individuals of each species. The average ratios, the proportion of small mammals in the diet, and the proportion of microhabitat use were transformed into the arc sine of their square root (Zar, 1996). A phylogenetic hypothesis (consensus of ten trees, 9237 steps) was used in the analysis below and was obtained from maximum linear parsimony using molecular characters (sub units 12S and 16S from mitochondrial rDNA and C-mos), with a total of 1278 base pairs (H. Zaher and F. Grazziotin, unpublished data). We chose not to include an outgroup in the comparative analyses due to the uncertainty surrounding this subject (Vidal et al., 2000; Zaher et al., 2009; Vidal et al., 2010; H. Ferrarezzi personal communication).

The relationship between the proportion of small mammals in diet and RBC, RHV and the proportion of individuals found on vegetation were analysed through linear regressions forced through the origin (i. e., with the intercept set to zero; see e. g. Midford et al., 2008) using independent contrasts (Felsenstein, 1985) generated for these variables using the PDAP:PDTree package of Mesquite software (Maddison and Maddison, 2009; Midford et al., 2008). We used the phylogeny of the tribe to generate the contrasts with all branch lengths set to one (Garland et al., 1992). In the analysis between contrasts of the proportion of small mammals in diet and circumference, the contrasts were also obtained using the branch lengths set as Grafen's method (Grafen, 1989). In this analysis the diagnosis test pointed out an unfitting of the data of proportion of small mammals in the diet when related to the branch lengths set as one. The calculation of independent contrasts eliminates the phylogenetic effect of the variables. Species and intermediate branches can be considered as independent points and can be used to analyze the evolutionary intrinsic correlation between quantitative characters (Martins and Garland, 1991; Diniz-Filho, 2000). Tests of the relationship between the proportion of small mammals in diet and morphology were made including *Drepanoides anomalus* and *Rhachidelus brazili* and, later, without them. Both species are robust, have a great head volume but do not eat mammals, which could influence the results.

Later, diet information, RBC and RHV were optimized in the phylogenetic hypothesis using the Mesquite software (Maddison and Maddison, 2009) through linear parsimony, with branch lengths set to one (Garland et al., 1992). The optimization or the character reconstruction allows us to formulate a possible evolutionary history of characters in any lineage. For diet, the optimization was done using discrete characters (e. g., lizard specialist, generalist), whereas for RBC and RHV we used continuous characters.

We included in our phylogeny the pseudoboines which were not on the original phylogeny taking into account their affinities with the species that were already included (see, e. g., Martins et al., 2001; Martins et al., 2002), using information from the literature (e. g., Zaher, 1994; Vidal et al., 2000; Zaher et al., 2009). We could not get a minimum of eight observations of microhabitat use for *Boiruna maculata*, *Clelia rustica*, *Mussurana quimi*, *Rhachidelus brazili* and *Siphlophis longicaudatus*. Thus, these species were not included in the test of the relationship between the proportion of use of vegetation and the proportion of small mammals in the diet. *Mussurana bicolor*, *P. guianensis*, *Phimophis iglesi* and *Pseudoboa newwiedii* were included only in morphological optimizations due to the scarcity of data regarding their ecology (Table 1). *Boiruna sertaneja* was included only in diet optimization.

RESULTS

Of the 33 species for which we obtained data on diet (Table 2), 29 eat lizards and 20 eat small mammals. Snakes were recorded in the diet of 18 species and birds in the diet of eight species. Amphibians, lizard eggs and bird eggs are occasionally found in the diet of pseudoboines (except for the species that are specialists in eggs). In those species that presented lizard or bird eggs as part of their diet, lizards and birds, respectively, were also consumed.

We obtained eight or more prey records for 22 species. Of these, nine were considered as generalists, i. e., no prey represented more than 70% of the total: *Boiruna maculata*, *Clelia clelia*, *C. rustica*, *Oxyrhopus melanogenys*, *O. petola*, *O. rhombifer*, *O. trigeminus*, *Pseudoboa coronata* and *P. haasi*. Small mammals and lizards were recorded in all these species (with proportions from about 10 to 60% for both prey types). Snakes were found in the diet of six of these generalist species (proportions from 2 to 58%) and birds in the diet of five of them, although in smaller proportions (2-25%). Amphibians and bird eggs were recorded, one of each, in the diet of one generalist species and lizard eggs in the diet of two, all of these in a proportion that did not exceed 5%.

Lizard specialization occurred in six species (*Phimophis guerini*, *Pseudoboa nigra*, *Siphlophis cervinus*, *S. compressus*, *S. longicaudatus*, and *S. pulcher*). Three species were considered as mammal specialists (*Mussurana quimi*, *Oxyrhopus clathratus* and *O. guibei*) and two as snake specialists (*Boiruna sertaneja* and *Clelia plumbea*). *Drepanoides anomalus* and *Rhachidelus brazili* were considered as lizard egg and bird egg specialists, respectively.

Regarding microhabitat use (Table 1), *Drepanoides anomalus* and *Siphlophis*

cervinus, *S. compressus* and *S. pulcher* were characterized as semi-arboreals (15% or more of the individuals found in activity on the vegetation).

Regarding morphology (Table 1), *Rhachidelus brazili* is the most robust species and has the largest head size. On the other hand, the genus *Siphlophis* comprises the species that have the smaller robustness and head size. *Boiruna maculata*, *Drepanoides anomalus*, *Phimophis guerini*, *P. guianensis* and *Mussurana* spp. showed moderate robustness and head size. The genus *Pseudoboa* comprises species with a moderate robustness and a small (*P. nigra*) to moderate head size (*P. coronata*, *P. haasi* and *P. neuwiedii*). *Clelia clelia*, *C. plumbea* and *C. rustica* have a moderate robustness and a small head size (*C. clelia* excluded). The genus *Oxyrhopus* comprises species with a small (*O. clathratus*, *O. guibei* and *O. petola*) to moderate robustness (*O. melanogenys*, *O. rhombifer* and *O. trigeminus*) and with a small (*O. clathratus* and *O. petola*) to moderate head size (*O. guibei*, *O. melanogenys*, *O. rhombifer* and *O. trigeminus*). *Phimophis iglesiasi* showed a great robustness and a moderate head size.

After removing the effect of phylogeny from our data, the regression between the contrasts, with and without including *Rhachidelus brazili* and *Drepanoides anomalus* in the analysis (oophagous species that eat prey that are also large, which could cause a bias in the result), indicate that the proportion of small mammals in the diet has no relationship with robustness in pseudoboine snakes ($r^2 = 0.003$, $P = 0.39$; $r^2 = 2.11$, $P = 0.47$, respectively). The same non significant result was found in the analysis between the proportion of small mammals in diet and relative head volume (with the oophagous species, $r^2 = 0.07$, $P = 0.12$; and without them, $r^2 = 0.03$, $P = 0.21$). Thus, an increase in the proportion of small mammals in diet seems to have no relationship with the evolution of robustness or head size in pseudoboines. When the contrasts were generated for the species that had both information, diet and microhabitat use, the regression between these contrasts failed to find a relationship between an increase in the use of vegetation and a decrease in the consumption of small mammals ($r^2 = 0.14$, $P = 0.07$), although the result was marginally non-significant.

The reconstruction of the evolutionary history of diet in pseudoboines (Fig. 1) indicates that lizard specialists (*P. guerini* and *P. nigra*) appeared independently at least twice during the diversification of the tribe. Since we did not use an outgroup in this analysis, it is impossible to know whether the species of *Siphlophis* kept the lizard specialization of the ancestor of the tribe or if it appeared as an independent event (and the ancestor was a generalist). Specialization in small mammals (*O. clathratus*, *O. guibei* and *M. quimi*) and snakes (*B. sertaneja* and *C. plumbea*) appeared independently each at least twice during the diversification of the tribe. The bird egg specialization seems to be an autapomorphy of *R.*

brazili. Lizard egg specialization is probably an autapomorphy of *D. anomalus*, but since the reconstruction of the diet of the immediate ancestor of this species shows an equivocal branch, we cannot be certain about it.

The optimization of RBC indicates that during the evolutionary history of pseudoboines, robustness decreased significantly in the ancestor of the genus *Siphlophis* and in *O. clathratus* and substantially increased in *R. brazili*. A slight decrease in robustness can be seen in *D. anomalus*, *B. maculata*, *C. plumbea* and *P. coronata* and a slight increase in *P. guerini*, in the genus *Mussurana*, *P. neuwiedii* and *P. nigra*. Due to the equivocal branches, it is not possible to know if robustness increased or not in *P. iglesiassi* (Fig. 2). In general, robustness seems to be very conservative among pseudoboines, being divided into three main clades: *Siphlophis* spp., *Oxyrhopus* spp. and the species from *C. rustica* to *P. haasi* in our phylogeny (Fig. 2).

The optimization of RHV indicates that head size substantially decreased in the ancestor of the genus *Siphlophis*, in *O. clathratus*, *O. petola* and *C. plumbea*. A significant increase in RHV seemed to have occurred in *P. guianensis* and *R. brazili* (Fig. 3). A slight decrease occurred in *C. rustica* and *P. nigra* and a slight increase occurred in the ancestor of *O. trigeminus* and *O. rhombifer*. Due to the equivocal branches, it is not possible to know if head size increased or not in *P. iglesiassi*, *D. anomalus*, *M. bicolor* and in *P. neuwiedii* and *P. coronata*, or if it decreased or not in *B. maculata* and *M. quimi* (Fig. 3).

DISCUSSION

The diet of pseudoboine snakes consists mainly of lizards and small mammals, as previously reported in the literature (e.g., Martins and Oliveira, 1998; Prudente et al., 1998; Bernarde and Abe, 2006). Andrade and Silvano (1996) suggested that an ontogenetic shift in diet occurs in *Oxyrhopus guibei*. However, like in *O. clathratus*, more than 70% of the diet of these species consists of small mammals and only 21% or less of lizards. This suggests that juveniles also feed on endothermic prey. On the other hand, we cannot rule out the possibility that our sample have underestimated the diet of juveniles and therefore, have caused a bias in our results.

Ophiophagy was occasionally recorded for some pseudoboine snakes (e.g., Vitt and Vangilder, 1983; Prudente et al., 1998; Pinto and Lema, 2002), and seems to be more important than previously thought. Pinto and Lema (2002), as well as the present study, found a generalist diet in *Boiruna maculata* and, curiously, its sister taxon, *B. sertaneja*, was considered a snake specialist. The same authors suggested a possible snake specialization for

Clelia plumbea, which was confirmed in our study. Our results confirmed a lizard specialization in four species of *Siphlophis* and probably in all species of the genus, in *Phimophis guerini*, and in *Pseudoboa nigra*, as well as specialization in lizard eggs in *Drepanoides anomalus* as already reported by the literature (e.g. Martins and Oliveira, 1998; Prudente et al., 1998; Sawaya, 2003). Among pseudoboines, *Drepanoides anomalus* and *Siphlophis* spp. are known to be semi-arboreal (e. g., Martins and Oliveira, 1998; Marques et al., 2001), which was confirmed by our study. Further, *Pseudoboa newwiedii* seems to often use the vegetation.

A robust body in snakes would help the accommodation of larger prey, decreasing prey interference in other physiological functions during the digestion process (Pough and Groves, 1983). Martins et al. (2002) suggest that mammal specialization is associated with a more robust body in snakes of the genus *Bothrops*. Our results indicate that the proportion of small mammals in diet is not related with robustness in pseudoboines. As mentioned before, robustness seems to be conservative among pseudoboines and many species in the tribe feed occasionally on small mammals. Maybe, the ancestor of the tribe had already an adequate robustness to allow a diet based on relative large prey. So robustness would not have been a limiting factor for the evolution of a diet based on mammals. In the future, the inclusion of an outgroup in these analyses will help to clarify this hypothesis. Furthermore, variations in robustness are known to reflect other selective agents (e. g., microhabitat; Martins et al., 2001). Indeed, L. Alencar (unpublished data) showed that microhabitat use also failed to explain the variation in robustness in pseudoboines.

The ingestion of large and/or wide prey seems also to be related with the size of the head in many species of snakes, which is generally larger in those species that feed on mammals. A larger head in snakes would make easier the ingestion process of this kind of prey (Greene, 1983; Pough and Groves, 1983; Shine, 1991). The regression between the contrasts of the proportion of small mammals in diet and head volume did not indicate any significant relationship between these two variables in pseudoboines. As in robustness, the evolution of a diet based on small mammals might not be limited by the size of the head in pseudoboines, if the ancestor already had an adequate head size for eating relatively large prey. Additionally, other selective pressures may have acted in the evolution of head size in pseudoboines (see below).

The tribe Pseudoboini seems not to be an adequate lineage to test the effects of vegetation use on the proportion of small mammals in the diet since the diet of the ancestors of arboreal forms is not known. Most arboreal pseudoboines are part of a single, basal lineage

(*Siphlophis* spp.) composed of lizard specialists. This diet specialization in this genus would probably be a consequence of phylogenetic inertia if the ancestor of the tribe was already a lizard specialist. Furthermore, there are lizard specialists among pseudoboines which do not use the vegetation or seldom use it and seem to have excluded mammals from their diets perhaps due to other reasons.

Pseudoboines have diverse feeding habits and most of this diversification occurred in terminal taxa. Through the reconstruction of the evolutionary history of diet, it seems that the ancestors of the species that are diet specialists were either specialists in the same type of prey or generalists. Queiroz and Rodriguez-Robles (2006) suggest that shifts in diet usually begin by incorporating a new type of prey as a less important diet component. These same authors showed that specialization in lizard and bird eggs tend to appear in those species whose ancestors fed on lizards and birds, respectively. The generalist species of pseudoboines feed mostly on small mammals, lizards, snakes, and birds. Probably their generalist ancestors also did so, which may have made mammal, lizard, and snake specialization in terminal taxa possible. Similarly, a generalist diet which included lizards and birds in the ancestors of *D. anomalus* and *R. brazili* probably favored the emergence of egg specialization in these species.

The evolution of robustness in pseudoboines seems to reflect phylogenetic inertia. Through the reconstruction, it is possible to note that robustness is divided basically into three clades, being the genus *Siphlophis* composed by those species with the smallest robustness, the genus *Oxyrhopus* by the moderately robust species and the remaining species that have the greater robustness values. The reconstruction of the evolutionary history of robustness also indicates that *Siphlophis* spp., which are lizards specialists, are considerably less robust than small mammal specialists and generalists, as we expected. On the other hand, the lizard specialists *Phimophis guerini* and *Pseudoboa nigra* have an equal or greater robustness than mammal specialists and the other generalist species. Additionally, *O. clathratus*, a small mammal specialist, is considered less robust than many species in the tribe, corroborating the finding that the evolution of a greater robustness was not associated with the evolution of an increase in the consumption of small mammals.

The large increase in robustness in *R. brazili* may be due to the fact that this species is a specialist in bird eggs. The consumption of this kind of prey probably requires a greater robustness because bird eggs have hard, calcareous shells and thus must be ingested as a whole. The lizard eggs specialist, *D. anomalus*, seems to have a similar robustness compared to mammal specialists and some generalists. Lizard eggs have in general more flexible shells

than those of bird eggs (see, e. g., Sexton et al., 2005) and this species has specialized teeth which break lizard eggs during swallowing (O. A. V. Marques, unpublished data). On the other hand, *R. brazili* has modifications in its anterior vertebrae which are used to break the calcareous shells of bird eggs (O. A. V. Marques, unpublished data). Unlike in *D. anomalus*, in *R. brazili* the entire egg reaches the esophagus, what could lead to a greater robustness in this species.

The reconstruction of head size in pseudoboines indicates a wide variation of the trend of this character among the species with the same and different feeding habits, including among mammal specialists. Since we failed to find any relationship between head size and the proportion of small mammals in the diet, this result was expected. An increase in head size in *Rhachidelus brazili* strengthens the hypothesis that a diet based on bird eggs imposes stronger pressures on morphology than other large prey. As mentioned before, lizard eggs have more flexible shells than bird eggs, what could explain the smaller head size in *Drepanoides anomalus* compared to *R. brazili*. The genus *Siphlophis* comprises snakes with relatively homogeneous head size (all of them small) and suggestively, all the species analyzed have semi-arboreal habits (with the exception of *S. longicaudatus*, which we were not able to get a minimum of microhabitat records). Lilliwhite and Henderson (1993) mentioned that head shape could be associated with microhabitat use, which could have prevented us to find a relationship between diet and head volume. However, L. Alencar (unpublished data) did not find any relationship between arboreality and head shape in pseudoboines. Further, an increase in head volume in *Phimophis guianensis* and the relative large head size in *P. iglesiasi*, species with apparently semi-fossorial habits (Rodrigues, 1993), contradicts the hypothesis that fossorial species tend to have smaller heads (Savitzky, 1983). Additionally, in L. Alencar (unpublished data), *P. guianensis* have the wider head among Pseudoboines and *P. iglesiasi* have a much more narrowed one. Thus, the possible selective pressures associated with changes in head size in pseudoboines remain obscure.

Our results show that pseudoboine snakes are highly diversified in their feeding habits, and that many types of specialization appeared during the evolutionary history of the lineage. Especially intriguing are the specializations in eggs of lizards and birds, which appeared each in a single taxon. Robustness varied relatively little during the evolutionary history of pseudoboines, indicating phylogenetic inertia. Additionally, the ancestor of the tribe could have been robust enough to eat small mammals. These two factors could have prevented us to detect an adaptative relationship between robustness and the proportion of small mammals in diet. Similarly, head size was not associated with an increase in small mammals in diet and

the possibility of an ancestor with an already large head which allowed the ingestion of small mammals could not be discarded. Unlike robustness, head volume varied widely among pseudoboines, what suggests that other selective agents have acted in the evolution of head size. The incorporation of an outgroup in future studies would help to clarify the relationships between morphology and diet in pseudoboines.

Acknowledgments.- We thank all the researchers that had contributed with information about the species studied and the scientific collections curators who provided access to specimens under their responsibility: F. L. Franco (IB), M. A. de Carvalho (UFMT), A. L. Prudente (MPEG), T. Grant (PUCRS), J. C. Moura-Leite (MHNCI) and G. Colli (UnB). We also thank P. Guimarães, A. Eterovic and L. Schiesari for critically reading the manuscript; O. A. V. Marques for providing *R. brazili* food data and for the suggestions during the development of this study. V. Germano for the help and helpful discussions during the analysis of the specimens deposited at IB. P. Valdujo, D. Guarda, R. Scartozzoni for the help with the analyses and C. Alencar for the help with the English translation. This study is part of the M.Sc. Thesis of LA and was funded by FAPESP (2007/56921-6 and 2006/58011-4).

LITERATURE CITED

- ANDRADE, R. O., AND R. A. SILVANO. 1996. Comportamento alimentar e dieta da falsa-coral *Oxyrhopus guibei* (Serpentes, Colubridae). *Revista Brasileira de Zoologia* 13:143-150.
- ARAÚJO, M. S., AND M. MARTINS. 2006. Defensive behavior in pit vipers of the genus *Bothrops* (Serpentes, Viperidae). *Herpetological Journal* 16:297-303.
- BARBOSA, A., AND E. MORENO. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. *The Auk* 116:712-725.
- BERNARDE, P. S., AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern Amazon, Brazil. *South American Journal of Herpetology* 1:102-113.
- BROOKS, D. R. AND D. A. MCLENNAN. 1991. Phylogeny, ecology and behavior: a research programme in comparative biology. University of Chicago Press, Chicago, Chicago, USA.
- CUNHA, O. R., AND F. P. NASCIMENTO. 1978. Ofídios da Amazônia X. As cobras da região leste do Pará, Belém. *Museu Paranaense Emílio Goeldi Publicações Avulsas* 31:1-218.
- CUNHA, O. R., AND F. P. NASCIMENTO. 1983. Ofídios da Amazônia XIX. As espécies de *Oxyrhopus* Wagler, com uma subespécie nova, e *Pseudoboa* Schneider, na Amazônia Oriental e Maranhão (Ophidia: Colubridae). *Boletim do Museu Paranaense Emílio Goeldi* 1:1-42.

- DINIZ-FILHO, J. A. F. 2000. Métodos filogenéticos comparativos. Holos, Ribeirão Preto, São Paulo, Brazil.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 1:1-15.
- GARCÍA-BERTHOU, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology* 70:708-711.
- GARLAND, T., JR., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18-32.
- GRAFEN, A. 1989. "The phylogenetic regression". *Philosophical Transactions of the Royal Society B* 326:119-157.
- GREENE, H. W. 1983. Dietary correlates of the origin and radiation of snakes. *American Zoologist* 23:431-441.
- HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, Oxford, UK.
- KLINGENBERG, C. P., AND W. EKAU. 1996. A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). *Biological Journal of the Linnean Society* 59:143-177.
- KOHLSDORF, T., T., JR. GARLAND, AND C. A. NAVAS. 2001. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology* 248:151-164.
- LILLYWHITE, H. B., AND R. W. HENDERSON. 1993. Behavioral and functional ecology of arboreal snakes. Pp. 1-48. In R. A. Seigel, and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, USA.
- LINDEMAN, P. V. 2008. Evolution of body size in the map turtles and sawbacks (Emydidae: Deirochelyinae: *Graptemys*). *Herpetologica* 64:32-46.
- MADDISON, W. P., AND D. R. MADDISON. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.7.1. Available at <http://mesquiteproject.org>.
- MARQUES, O. A. V., A. ETEROVIC, AND I. SAZIMA. 2001. Serpentes da Mata Atlântica: guia ilustrado para a Serra do Mar. Holos Editora, Ribeirão Preto, São Paulo, Brazil.
- MARQUES, O. A. V., A. ETEROVIC, I. SAZIMA, AND C. STRUSSMANN. 2005. Serpentes do Pantanal: Guia Ilustrado. Holos Editora, Ribeirão Preto, São Paulo, Brazil.
- MARTINS, E. P., AND T., JR. GARLAND. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* 45:534-557.
- MARTINS, E. P., AND T. F. HANSEN. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. Pp. 22-75. In E. P. Martins

- (Eds.), *Phylogenies and the comparative method in animal behavior*. Oxford University Press, New York, New York, USA.
- MARTINS, M., AND E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78-150.
- MARTINS, M., M. S. ARAÚJO, R. J. SAWAYA, AND R. NUNES. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). *Journal of Zoology (London)* 254:529-538.
- MARTINS, M., O. A. V. MARQUES, AND I. SAZIMA. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. Pp. 307-328. *In* G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- MIDFORD, P. E. T., T., JR. GARLAND, AND W. P. MADDISON. 2008. PDAP package of Mesquite. Version 1.14.
- PIANKA, E. R. 2000. *Evolutionary Ecology*. Benjamin-Cummings, Addison-Wesley-Longman, San Francisco, California, USA.
- PINTO, C., AND T. LEMA. 2002. Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). *Iheringia* 92:9-19.
- PIZZATTO, L., AND O. A. V. MARQUES. 2002. Reproductive biology of the false coral *Oxyrhopus guibei* (Colubridae) from Southeastern Brazil. *Amphibia-Reptilia* 23:495-504.
- PIZZATTO, L., S. M. ALMEIDA SANTOS, AND R. SHINE. 2007a. Life-history adaptations to arboreality in snakes. *Ecology* 88:359-366.
- PIZZATTO, L., O. A. V. MARQUES, AND M. MARTINS. 2007b. Ecomorphology of boine snakes, with emphasis on South American forms. Pp. 254-269. *In* R. W. Henderson (Org.), *Biology of Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- POUGH, F. H., AND J. D. GROVES. 1983. Specializations of the body form and food habits of snakes. *American Zoologist* 23:443-454.
- PRUDENTE, A. L. C., J. C. MOURA-LEITE, AND S. A. A. MORATO. 1998. Alimentação das espécies de *Siphlophis* Fitzinger (Serpentes, Colubridae, Xenodontinae, Pseudoboini). *Revista Brasileira de Zoologia* 15:375-383.
- QUEIROZ, A., AND J. A. RODRÍGUEZ-ROBLES. 2006. Historical contingency and animal diets: the origin of egg eating in snakes. *The American Naturalist* 167:684-694.
- RODRIGUES, M. T. 1993. Herpetofauna of paleoquaternary sand dunes of the middle São Francisco River: Bahia: Brazil. VI. Two new species of *Phimophis* (Serpentes: Colubridae)

- with notes on the origin of Psammophilic adaptations. *Papéis Avulsos de Zoologia* 38:187-198.
- SAVITZKY, A. 1983. Coadapted character complexes among snakes: fossoriality, piscivory and durophagy. *American Zoologist* 23:397-409.
- SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.
- SEXTON, O. J., J. E. BRAMBLE, I. L. HEISLER, C. A. PHILLIPS, AND D. L. COX. 2005. Eggshell composition of squamate reptiles: relationship between eggshell permeability and amino acid distribution. *Journal of Chemical Ecology* 31:2391-2401.
- SHINE, R. 1991. Why do larger snakes eat larger prey items?. *Functional Ecology* 5:493-502.
- TEIXEIRA, I., AND S. T. BENNEMANN. 2007. Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. *Biota Neotropica* 7:67-76.
- UETZ, P. 2007. The new reptile database. Available at [HTTP://www.reptile-database.org](http://www.reptile-database.org). Zoological Museum Hamburg, Hamburg, Hamburg, Germany.
- VIDAL, N., S. G. KINDL, A. WONG, AND S. B. HEDGES. 2000. Phylogenetic relationships of Xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. *Molecular Phylogenetics and Evolution* 14:389-402.
- VIDAL, N., M. DEWYNTER, AND D. J. GOWER. 2010. Dissecting the major American snake radiation: A molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies* 333:48-55.
- VINCENT, S. E., P. D. DANG, A. HERREL, AND N. J. KLEY. 2006. Morphological integration and adaptation in the snake feeding system: a comparative phylogenetic study. *Journal of Evolutionary Biology* 19:1545-1554.
- VINCENT, S. E., M. C. BRANDLEY, A. HERREL, AND M. E. ALFARO. 2009. Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. *Journal of Evolutionary Biology* 22:1203-1211.
- VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* 4:273-296.
- ZAHER, H. 1994. Phylogenie des Pseudoboini et evolution des Xenodontinae sud-américains (Serpentes, Colubridae). P.h.D. Dissertation, Muséum National D'Histoire Naturelle, Paris, France.
- ZAHER, H., F. G. GRAZZIOTIN, J. E. CADLE, R. W. MURPHY, J. C. MOURA-LEITE, AND S. L. BONATTO. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with

emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia* 49:115-153.

ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey, USA.

TABLE 1.— Relative body circumference (RBC), relative head volume (RHV), proportion of small mammals in diet (Mam) and microhabitat use (Mic, proportion of individuals found in activity on vegetation) of pseudoboine snakes. SD = Standard deviation; N = sample size. Morphological data multiplied by 1000.

	RBC		RHV		Mam	Mic
	($\bar{x} \pm \text{SD}$)	N	($\bar{x} \pm \text{SD}$)	N		
<i>Boiruna maculata</i>	74 $\pm$ 8	28	15.5 $\pm$ 1.2	26	0.13	-
<i>Clelia clelia</i>	79 $\pm$ 5	5	-	-	0.17	0.07
<i>Clelia plumbea</i>	74 $\pm$ 8	24	14.4 $\pm$ 1.1	23	0.11	0.00
<i>Clelia rustica</i>	83 $\pm$ 10	20	14.8 $\pm$ 1.7	20	0.50	-
<i>Drepanoides anomalus</i>	76 $\pm$ 6	10	16.9 $\pm$ 1.5	9	0.00	0.15
<i>Mussurana bicolor</i>	88 $\pm$ 4	7	17.2 $\pm$ 1.4	6	-	-
<i>Mussurana quimi</i>	87 $\pm$ 7	21	15.6 $\pm$ 1.3	20	0.75	-
<i>Oxyrhopus clathratus</i>	63 $\pm$ 5	20	13.5 $\pm$ 1.3	20	0.82	0.00
<i>Oxyrhopus guibei</i>	71 $\pm$ 7	20	15.2 $\pm$ 1.2	20	0.77	0.05
<i>Oxyrhopus melanogenys</i>	73 $\pm$ 9	27	15.0 $\pm$ 1.4	27	0.46	0.03
<i>Oxyrhopus petola</i>	68 $\pm$ 6	21	13.6 $\pm$ 1.1	22	0.30	0.03
<i>Oxyrhopus rhombifer</i>	77 $\pm$ 8	18	16.3 $\pm$ 1.8	20	0.49	0.04
<i>Oxyrhopus trigeminus</i>	75 $\pm$ 10	21	16.2 $\pm$ 1.4	21	0.33	0.00
<i>Phimophis guerini</i>	85 $\pm$ 11	22	15.3 $\pm$ 1.8	23	0.08	0.00
<i>Phimophis guianensis</i>	84 $\pm$ 12	6	16.9 $\pm$ 1.6	6	-	-
<i>Phimophis iglesiassi</i>	96 $\pm$ 10	7	17.1 $\pm$ 1.0	7	-	-
<i>Pseudoboa coronata</i>	76 $\pm$ 8	19	16.1 $\pm$ 1.2	18	0.27	0.00
<i>Pseudoboa haasi</i>	81 $\pm$ 8	20	15.2 $\pm$ 1.0	20	0.60	0.00
<i>Pseudoboa neuwiedii</i>	85 $\pm$ 10	10	16.2 $\pm$ 1.0	10	-	0.11
<i>Pseudoboa nigra</i>	85 $\pm$ 10	20	14.9 $\pm$ 1.1	20	0.05	0.07
<i>Rhachidelus brazili</i>	108 $\pm$ 13	20	19.6 $\pm$ 1.9	23	0.00	-
<i>Siphlophis cervinus</i>	54 $\pm$ 6	18	12.7 $\pm$ 1.0	17	0.05	0.64
<i>Siphlophis compressus</i>	54 $\pm$ 5	20	12.6 $\pm$ 1.2	21	0.00	0.29
<i>Siphlophis longicaudatus</i>	53 $\pm$ 8	20	12.9 $\pm$ 1.2	18	0.00	-
<i>Siphlophis pulcher</i>	57 $\pm$ 8	16	12.6 $\pm$ 0.8	12	0.00	0.25

TABLE 2 – Proportion of prey items recorded for Pseudoboine snakes; n = total number of preys.

	Mammals	Lizards	Snakes	Birds	Amphibians	Bird eggs	Lizard eggs	Other	N
<i>Boiruna maculata</i>	0.13	0.10	0.58	0.16				0.03	31
<i>Boiruna sertaneja</i>		0.29	0.71						14
<i>Clelia clelia</i>	0.17	0.27	0.50	0.02				0.02	40
<i>Clelia langeri</i>	1								1
<i>Clelia plumbea</i>	0.11	0.16	0.74						19
<i>Clelia rustica</i>	0.50	0.10	0.40						10
<i>Drepanoides anomalus</i>		0.12					0.87		9
<i>Mussurana bicolor</i>	0.17	0.17	0.17		0.50				6
<i>Mussurana montana</i>		0.50	0.50						2
<i>Mussurana quimi</i>	0.75	0.12	0.12						8
<i>Oxyrhopus clathratus</i>	0.82	0.12		0.06					34
<i>Oxyrhopus guibei</i>	0.77	0.21		0.02					43
<i>Oxyrhopus melanogenys</i>	0.46	0.46		0.06			0.02		52
<i>Oxyrhopus petola</i>	0.30	0.35		0.25	0.05	0.05			20
<i>Oxyrhopus rhombifer</i>	0.49	0.49	0.02						41
<i>Oxyrhopus trigeminus</i>	0.33	0.56		0.08			0.03		36
<i>Oxyrhopus vanidicus</i>	0.50	0.50							6
<i>Phimophis guerini</i>	0.08	0.92							12

<i>Phimophis iglesi</i>	1					3
<i>Phimophis scitarcibatus</i>	1					2
<i>Pseudoboa coronata</i>	0.27	0.45	0.18			11 0.09
<i>Pseudoboa haasi</i>	0.60	0.13	0.20			15 0.07
<i>Pseudoboa martinsi</i>			1			1
<i>Pseudoboa neuwiedii</i>	0.25	0.50	0.25			4
<i>Pseudoboa nigra</i>	0.05	0.86	0.02	0.02	0.05	56
<i>Rhachidelus brazili</i>				0.14	0.86	14
<i>Siphlophis cervinus</i>	0.05	0.82	0.13	0.05		38
<i>Siphlophis compressus</i>		0.96	0.04			26
<i>Siphlophis leucocephalus</i>		1				1
<i>Siphlophis longicaudatus</i>		0.77	0.23			13
<i>Siphlophis pulcher</i>		0.83	0.10		0.07	30
<i>Siphlophis worontzowi</i>		0.83		0.17		6

Fig. 1.—Reconstruction of diet in Pseudoboine snakes.

Fig. 2.—Reconstruction of robustness (RBC) in Pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Fig. 3.—Reconstruction of head volume (RHV) of Pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Capítulo 2

MORPHOLOGICAL ADAPTATIONS TO ARBOREALITY IN SNAKES: A CASE STUDY WITH A NEOTROPICAL LINEAGE

LAURA R. V. ALENCAR^{1,2}, MARÍLIA P. GAIARSA¹, AND MARCIO MARTINS¹

¹*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, São Paulo, SP, Brasil, CEP 05508-090*

²CORRESPONDENCE: laura.alencar@globocom

ABSTRACT: Adaptative relationships between morphology and arboreality have been suggested for some snake groups. For instance, there is strong evidence that the adoption of arboreal habits tend to lead to slender bodies and longer tails. Here we explore some of these possible associations using the Neotropical snake tribe Pseudoboini. Specifically, we aimed to test whether the evolution of semi-arboreal habits in pseudoboines was associated with changes in body size, tail length, robustness, head shape, and in the number of vertebrae per unit body. These hypotheses were tested using raw data as well as independent contrasts. By optimizing characters on a phylogeny of the tribe, we also inferred how semi-arboreal habits evolved and the morphological changes occurred during the diversification of the tribe. Microhabitat reconstruction indicated that semi-arboreal habits evolved at least twice during the diversification of the tribe. We failed to find any association between arboreality and morphological features such as body size, robustness, head shape, and the number of vertebrae per body unit. However, a positive association was found between tail length and vegetation use. These absences of relationships could be related to phylogenetic inertia in some morphological traits, conflicts between diet and arboreality imposed on morphology, an ancestral morphology which was already adequate for arboreal habits, or even the action of alternative selective agents.

Key Words: Arboreality; Microhabitat, Adaptative Evolution; Pseudoboini.

THE MORPHOLOGY of an organism can be tightly associated to the environment it occupies, providing insights on the ecological and evolutionary adjustments between the phenotype and the environment (Rickfles and Miles, 1994). The independently repeated evolution of a morphological trait in species that use similar environments implies that natural selection caused these changes, because genetic drift is unlikely to result in concordant evolutionary transformations (Schluter and Nagel, 1995; Richmond and Reeder, 2002). Thus, morphological convergence has provided some of the most compelling tests of adaptative evolution (Schluter, 2000; Vincent et al., 2009) and has been explored in different groups of animals (e.g. Losos, 1992; Winemiller et al., 1995; Vincent et al., 2009). In snakes, species that use different microhabitats can be included in different morphological syndromes (e.g. Martins et al., 2001, Pizzatto et al., 2007*b*). The evolution of arboreality in snakes offers an interesting opportunity to examine the morphological adaptations related to the arboreal microhabitat, especially due to the constraints imposed by this physically challenging environment.

Arboreal habits evolved in several snake lineages, and many of these show similar morphological specializations (Cadle and Greene, 1993; Lillywhite and Henderson, 1993). These specializations have been considered as adaptations to the physical limitations imposed by the arboreal microhabitat (see Lillywhite and Henderson, 1993; Martins et al., 2001). Lillywhite and Henderson (1993) suggested that snakes which use the vegetation more frequently tend to be smaller than those that do not use the vegetation at all. This is probably due to the physical limitations imposed by gravity when a snake assumes a vertical posture in this microhabitat. More arboreal snakes also tend to have longer tails and a more slender body when compared to snakes that use other microhabitats (e.g. Guyer and Donnelly, 1990; Cadle and Greene, 1993; Lillywhite and Henderson, 1993; Martins et al., 2001; Pizzatto et al., 2007*a, b*). An increase in tail length and a decrease in robustness in arboreal snakes would be adaptations to displacement and equilibrium in the arboreal microhabitat. Further, a less robust body could also favor a better crypsis for snakes in this microhabitat (Lillywhite and Henderson, 1993; Pizzatto et al., 2007*a*). Lillywhite and Henderson (1993) also suggested that arboreal snakes tend to have narrower skulls and elongate snouts, which could favor binocular vision.

Another trait that could be related to arboreality in snakes is the number of body vertebrae. Body vertebrae, along with the ribs, connective tissues, and axial muscles, form an interactive unit that is responsible for locomotion (Jayne, 1988; Kelley et al., 1997). Arboreal snakes tend to have longer segments of the axial musculature in relation to, as an example,

aquatic snakes. The tendon from a single segment of the axial musculature may exceed 30 vertebrae in certain arboreal species compared with only six in some aquatic species (see Jayne, 1982; Lillywhite and Henderson, 1993). An increase in the segments of the axial musculature would favor the locomotion and body mass support in arboreal microhabitats. Additionally, there is evidence that the number of body vertebrae is related to the lateral bending capacity of snakes (e.g. Jayne, 1982; Lillywhite and Henderson, 1993; Kelley et al., 1997; Jayne and Riley, 2007). Therefore, natural selection would favor an increase in the number of body vertebrae in snakes that frequently use the vegetation. This condition could be an advantage in microhabitats that are discontinuous, irregular, and with few points of support like the arboreal microhabitat. However, the number of ventral scales, which corresponds to the number of body vertebrae in many snake species, has been the focus of only a few studies concerning snake morphology and arboreality (e.g. Lindell, 1994; Pizzatto et al., 2007a) and remains poorly explored.

Here we explore some of the possible ecomorphological associations above using the tribe Pseudoboini as a model lineage. This tribe represents a monophyletic group (e.g. Jenner and Dowling, 1985; Vidal et al., 2000; Zaher et al., 2009; Vidal et al., 2010) which includes semi-arboreal, terrestrial and even semi-fossorial forms (Rodrigues, 1993; Martins and Oliveira, 1998; L. Alencar, unpublished data). Specifically, we aimed to test whether the evolution of semi-arboreal habits in pseudoboines was associated with changes in body size, tail length, robustness, head shape, and in the number of vertebrae per unit body. These hypotheses were tested using raw data as well as independent contrasts. By optimizing characters on a phylogeny of the tribe, we also inferred how semi-arboreal habits evolved and the morphological changes occurred during the diversification of the tribe.

MATERIALS AND METHODS

Microhabitat data

Information about microhabitat use of pseudoboine snakes were obtained by gathering data in the literature and in scientific collections, as well as observations granted by other researchers (L. Alencar, unpublished data; appendix III). Only data obtained for snakes that were active during field observations were included in microhabitat analyses. We used only species for which at least eight observations of microhabitat use were available (Table 1). We assume that eight observations for each species are sufficient to characterize its main microhabitat. Species were classified as semi-arboreals (proportion of individuals found in activity on vegetation equal or greater than 0.15) and non arboreals. Although arbitrary, this

distinction decreases the chance of considering a species as semi-arboreal when it only rarely uses the vegetation (Martins et al., 2001).

Morphological data

Since adult female samples were small, we only used morphometric and scale count data from adult males. For each preserved specimen we measured snout-vent length (SVL), mid body circumference (Circ), head width, and head length (to infer head shape), using a measuring tape (1 mm) and a dial caliper (0.1 mm). We also counted the number of ventral (Nvs) and subcaudal scales (Nsc) for each specimen. SVL was used to explore the hypothesis that the more arboreal a snake is, smaller is its body size. The ratio between circumference and SVL (RCirc) was used as a proxy for species robustness (see García-Berthou, 2001). RCirc was used to test whether robustness decreases in relation to an increase in arboreality. The ratio between head width and head length (head shape) was used to test the hypothesis that the more arboreal a snake is, the narrower is its head. We used the Nvs/SVL ratio (RNvs) to explore a possible association between vegetation use and an increase in the number of vertebrae per body unit. Since the number of subcaudal scales covaried with the number of ventral scales (L. Alencar, unpublished data), we used the ratio between these two variables (RNsc) to evaluate the effect of vegetation use on tail length. Only species for which at least five individuals could be measured were included in the analyses (Table 1).

Analyses

For all analyses, SVL measures were transformed to their natural log. All ratios and the proportion of individuals found on vegetation were transformed to the arc sine of their square root (Zar, 1996). The phylogenetic hypothesis (consensus of ten trees, 9237 steps) was obtained from maximum linear parsimony using molecular characters (sub units 12S and 16S from mitochondrial rDNA and C-mos), with a total of 1278 base pairs (H. Zaher and F. Grazziontin, unpublished data). We chose not to include an outgroup in the comparative analyses due to the uncertainty surrounding the identity of the sister group of pseudoboines (Vidal et al., 2000; Zaher et al., 2009; Vidal et al., 2010; H. Ferrarezzi personal communication).

We compared SVL, RNsc, RCirc, head shape, and RNvs between semi-arboreal and non-arboreal species using a Student *t*-test in Statistica 7.0 (StatSoft, 2005). Possible adaptative relationships between morphology and the proportion of vegetation use were analyzed through linear regressions forced through the origin (i. e., with the intercept set to

zero; see e. g. Midford et al., 2008), using independent contrasts (Felsenstein, 1985) generated for these variables using the PDAP:PDTree package of Mesquite program (Midford et al., 2008; Maddison and Maddison, 2009). We used the tribe phylogeny to generate the contrasts with all branch lengths set to one (Garland et al., 1992). In the analysis between the contrasts of RCirc and the proportion of vegetation use, the diagnosis test pointed out an unfitting of the data of RCirc when related to the branch lengths set as one. So, these contrasts were obtained using the method of arbitrary branch lengths (Pagel, 1992).

The probable evolutionary histories of SVL, RNsc, head shape, RNvs and microhabitat use of pseudoboine snakes were reconstructed through linear parsimony on the phylogeny, using the Mesquite software (Maddison and Maddison, 2009), with branch lengths set to one (Garland et al., 1992). The optimizations or the character reconstructions of the morphological variables were done using continuous characters whereas for microhabitat use we used discrete characters (e.g. semi-arboreals and non-arboreal). The optimization of RCirc will be published elsewhere and is not presented here.

We included in our phylogeny the pseudoboines which were not included in the original phylogeny. We did it by taking into account their affinities with the species that were already included (see, e. g., Martins et al., 2001; Martins et al., 2002), using information from the literature (e. g., Zaher, 1994; Vidal et al., 2000; Zaher et al., 2009). We could not measure Nsc and head shape in a minimum of five individuals of *Clelia clelia*. Thus, this species was not included in the analyses related to these variables. *Boiruna maculata*, *Clelia rustica*, *Mussurana bicolor*, *Mussurana quimi*, *Phimophis guianensis*, *Rhachidelus brazili*, and *Siphlophis longicaudatus* were included only in the morphological reconstructions. *Phimophis iglesiasi* is the sister-group of all other pseudoboines; thus, including this species in the reconstructions allowed the evaluation, with a greater support, of character evolution in the ancestor of *Siphlophis*, which is the group with most semi-arboreal species, as well as character evolution in the tribe as a whole (see phylogeny). For this reason, although we could not get eight observations of microhabitat use for *P. iglesiasi*, we included this species in the Student *t*-tests and in microhabitat reconstruction. Based on literature data and observations by other researchers (e.g. Rodrigues, 1993, 2003; P. Valdujo personal communication), *P. iglesiasi* is a semi-fossorial species, and thus considered as non-arboreal in this study.

RESULTS

Our results indicate that *Siphlophis cervinus*, *S. compressus*, *S. pulcher* and *Drepanoides anomalus* are semi-arboreals (Table 1; L. Alencar, unpublished data) and that

semi-arboreal habits appeared at least twice during the diversification of the tribe. The reconstruction of microhabitat also indicates that the ancestor of the tribe was a non-arboreal species (Fig. 1).

Phimophis iglesi and *P. guianensis* are the smallest species, while *C. plumbea* and *C. clelia* are the largest ones (Table 1, Fig. 2). Semi-arboreals are significantly smaller than non-arboreals ($t = 4.26$, $DF = 337$, $P < 0.001$). Among semi-arboreals, *D. anomalus* has the smaller SVL, and *S. pulcher*, *S. cervinus*, and *S. compressus* are relatively small (Table 1, Fig. 2). After removing the effect of phylogeny, we found no effect of the use of vegetation on body size in pseudoboines ($r^2 = 0.05$, $P = 0.18$). The character optimization indicates that SVL decreased substantially in *P. guianensis* and increased substantially in *C. rustica* and in the ancestor of *C. clelia* and *C. plumbea* (Fig. 3).

Pseudoboa nigra and *P. coronata* are the species with the greatest RNsc, while *P. iglesi* and *C. rustica* are those with the smallest values of RNsc (Table 1, Fig. 4). The tail is significantly longer in semi-arboreals compared to non-arboreals ($t = 6.87$, $DF = 311$, $P < 0.001$) and all semi-arboreals have relatively long tails (Table 1, Fig. 4). The evolution of the semi-arboreal habit seems to have led to the evolution of longer tails in pseudoboines ($r^2 = 0.17$, $P = 0.05$). The reconstruction of tail length indicates that it decreased significantly in *C. rustica*, *B. maculata*, and *P. haasi*, and increased substantially in the ancestor of the genus *Siphlophis*, *O. petola*, *D. anomalus*, *R. brazili* and in the ancestor of the genus *Pseudoboa* (Fig. 5).

Regarding RCirc, *Siphlophis* spp. are the less robust species and *R. brazili* is the most robust form (Table 1, Fig. 6). Semi-arboreals are less robust ($t = 12.16$, $DF = 316$, $P < 0.001$). Among semi-arboreals, only the species of *Siphlophis* seem to be less robust. However, *D. anomalus* is less robust than the other species in its clade (Table 1, Fig. 6). Concerning head shape, *Oxyrhopus rhombifer* and *M. bicolor* have the relatively narrower heads, whereas *P. guianensis* is the species with the relatively wider head (Table 1, Fig. 7). Semi-arboreals have a relatively wider head compared to non-arboreals ($t = 2.36$, $DF = 308$, $P = 0.01$). Among semi-arboreals, *Siphlophis* spp. have relatively wider heads and *D. anomalus* a narrow one (Table 1, Fig. 7). However, both robustness and head shape do not seem to vary greatly among pseudoboines. Using independent contrasts, we did not find an effect of the use of vegetation on robustness and head shape ($r^2 = 0.007$, $P = 0.36$; $r^2 = 0.11$, $P = 0.1$, respectively). The reconstruction of head shape indicates that head width decreased substantially in *P. neuwiedii* and increased substantially in *S. compressus*, *P. guianensis*, and *Boiruna maculata* (Fig. 8; reconstruction of robustness will be published elsewhere).

Phimophis iglesiasi has the greatest number of vertebrae per body unit (RNvs), while *C. clelia* and *C. plumbea* have the lowest (Table 1, Fig. 9). Semi-arboreals have a greater RNvs when compared to non-arboreals ($t = 9.31$, $DF = 323$, $P < 0.001$). All semi-arboreals have relatively large RNvs (Table 1; Fig. 9). However, the regression using independent contrasts does not indicate a strong effect of the use of vegetation on the number of vertebrae per body unit, although the result was marginally non-significant ($r^2 = 0.12$, $P = 0.08$). The reconstruction of RNv indicates that the number of vertebrae per body unit decreased substantially in *C. rustica*, in the ancestor of *C. clelia* and *C. plumbea*, and in *Pseudoboa haasi*. On the other hand, it increased in the ancestor of *O. trigeminus* and *O. rhombifer*, in *O. melanogenys* and in *P. guianensis* (Fig. 10).

DISCUSSION

Our results indicate that the ancestor of pseudoboines was a terrestrial species. The semi-arboreal habit evolved at least twice during the diversification of the tribe. However, it seems that a third independent appearance of semi-arboreal habits occurred in pseudoboines, since the few field observations on active individuals of *O. occipitalis* indicate that it is semi-arboreal (e.g. Martins and Oliveira, 1998).

Although conventional comparisons indicated that semi-arboreal species have smaller body sizes than non-arboreals, the analyses using the independent contrasts failed to show an effect of the use of vegetation on body size among pseudoboines. The species of *Siphlophis* do not reach a large body size but seem to be relatively larger than *D. anomalus* and some non-arboreal species. Body size is frequently a target of natural selection due to its strong implications in an animal's physiology and life history (Richmond and Reeder, 2002). Thus, selective pressures unrelated to semi-arboreal habits may have favored a decreases (e.g. *Phimophis guianensis*) and/or increases (e.g. *Clelia clelia* and *Clelia plumbea*) in body size among pseudoboines. An increase of body size in males could reflect the presence of male-male combat (e.g. Shine, 1978). However, so far this behavior has not been reported for pseudoboines. The absence of an obvious effect of arboreality on body size was also reported by Martins et al. (2001) and Pizzatto et al. (2007a, b). Lillywhite and Henderson (1993) suggested that there may be an upper limit of body size for arboreal snakes due to physiological constraints, whereas Pizzatto et al. (2007a, b) argue that phylogenetic inertia may be responsible for the absence of this effect in boas and pythons.

The use of vegetation in pseudoboines seems to have led to an increase in tail length, as indicated by studies on other snake lineages (e.g. Martins et al., 2001; Pizzatto 2007a, b).

The size of the tail is highly variable among species and clades of pseudoboines. Besides the semi-arboreal species, some species considered as non-arboreal (*O. petola*, *R. brazili*, *P. neuwiedii*, *P. coronata* and *P. nigra*) also have long tails. Longer tails in non-arboreal snakes could be related to foraging strategies (see Strüssmann and Sazima, 1990) or defensive behavior (see Greene, 1988; Guyer and Donnelly, 1990). Curiously, tail length seemed to drastically decrease in largest species of pseudoboines, *C. rustica*, *B. maculata*, and *P. haasi*. The size of the tail may enhance the fitness of male snakes by providing space for larger hemipenes and/or by enhancing a male's ability to obtain mates (King, 1989; Shine et al., 1999). Since we used only males in our analyses, we could not discard a possible influence of sexual selection in the evolution of tail length in pseudoboines.

Contrary to the results obtained by Martins et al. (2001) and Pizzatto et al. (2007a, b), our analyses using independent contrasts failed to indicate an effect of arboreality on robustness in pseudoboine snakes. Robustness seems to be a conservative trait in the tribe (L. Alencar, unpublished data; this study) and could reflect other selective pressures (e. g. diet, Martins et al., 2002). However, L. Alencar (unpublished data) also failed to find any effect of the consumption of larger prey (small mammals) on robustness in pseudoboines. Although conventional comparisons indicated that semi-arboreal species are less robust, probably this is due to the fact that *Siphlophis* spp. are much slender than the other pseudoboines. Furthermore, the semi-arboreal *D. anomalus* is as or more robust than many species in the tribe, what could reflect its specialized diet in lizard eggs (L. Alencar, unpublished data). Thus, a diet based on eggs seems to have constrained a decrease in robustness in *D. anomalus*. Conflicting selective pressures acting on morphology were also suggested by Kohlsdorf et al. (2008) in a lineage of lizards. These authors studied the conflicts imposed by a diet based on “hard prey” and those imposed by locomotion in different habitat types on the head morphology of tropidurid lizards.

Lillywhite and Henderson (1993) suggested that more arboreal snakes tend to have narrower skulls and longer snouts. However, conventional comparisons indicated that semi-arboreal pseudoboines have larger heads than the non-arboreal forms. Furthermore, when the effect of phylogeny was removed, we failed to find any evidence of the effect of arboreal habits on head width. In fact, the only substantial decrease in head width occurred in the terrestrial *P. neuwiedii*. Although head size varies widely among pseudoboines (L. Alencar, unpublished data), the present study indicates that head shape seems to be conservative in the tribe.

The number of vertebrae per body unit is highly variable in pseudoboine snakes. Although we failed to find an effect of arboreality on the number of vertebrae per body unit when using independent contrasts, we found that semi-arboreal species have a higher number of body vertebrae when compared to many other species. Perhaps the ancestor of the tribe already had many body vertebrae, for another reason than semi-arboreal habits, which could have masked a possible effect of the semi-arboreal habit on vertebrae number. The future inclusion of an outgroup in this analysis would help to test this hypothesis. Our reconstruction of the number of vertebrae per body unit indicates that, after the *Siphlophis* clade diverged, the number of body vertebrae decreased and increased again only in terminal taxa, which include non-arboreal species (e.g. *O. trigeminus*, *O. rhombifer*, *O. melanogenys*). Constriction, or simply handling prey using body coils, has been observed in many pseudoboines (e. g., Andrade and Silvano, 1996; Martins and Oliveira, 1998). Constriction has been shown to be related with an increase in the number of body vertebrae in snakes, which may facilitate body bending (Jayne, 1982; Lindell, 1994), what could explain part of the variation of this trait among pseudoboines. Future studies using different snake lineages, in which the arboreal habit evolved independently many times, would help to elucidate the eventual effect of arboreality on the number of body vertebrae in snakes. Curiously, *P. iglesiasi* and *P. guianensis* have many vertebrae per body unit, contradicting the hypothesis that semi-fossorial snakes tend to have fewer body vertebrae than species occupying other microhabitats (Lindell, 1994). However, inferences about the semi-fossorial habit of these two species (Rodrigues, 1993, 2003) are based upon only a few observations of individuals in the wild and thus this conclusion should be considered cautiously.

Removing the effect of phylogeny from our analyses, we failed to find apparent causal relationships between arboreality and most morphological features we considered in pseudoboines. The apparent absence of an effect of arboreality on robustness was probably due to phylogenetic inertia or to the constraints imposed on robustness by a diet based on eggs in *D. anomalus*. Our results do not support the hypothesis that more arboreal snakes would tend to have narrower heads. On the contrary, most semi-arboreal pseudoboines have larger heads. However, the lack of evidence of some adaptative relationships remain doubtful (e. g. number of vertebrae per body unit and arboreality), and the inclusion of an outgroup in the analyses would help to test these hypotheses. Finally, a decrease in body size, as well as increases in tail length and in the number of vertebrae per body unit, in non-arboreal pseudoboines indicates that other selective agents have played important roles in the evolution of these traits in this lineage.

Acknowledgments.- We thank all researchers that contributed with information about the species studied, and the curators of scientific collections who provided access to specimens under their responsibility: F. L. Franco (IB), H. Zaher (MZUSP), M. A. de Carvalho (UFMT), A. L. Prudente (MPEG), T. Grant (PUCRS), J. C. Moura-Leite (MHNCI) and G. Colli (UnB). Hussam Zaher and F. Grazziotin kindly provided the phylogeny and taxonomic information. We also thank P. Valdujo for helpful discussions, D. Guarda, R. Scartozzoni for the help with the analyses and V. Germano for the help during the selection and examination of the specimens deposited at IB. This study is part of the M.Sc. thesis of LA and was funded by FAPESP (2007/56921-6 and 2006/58011-4).

LITERATURE CITED

- ANDRADE, R. O., AND R. M. SILVANO. 1996. Comportamento alimentar e dieta da “falsacoral” *Oxyrhopus guibei* Hoge & Romano (Serpentes, Colubridae). *Revista Brasileira de Zoologia* 13:143-150.
- CADLE, J. E., AND H. W. GREENE. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281-293. *In* R. E. Ricklefs, and D. Schluter (Eds.), *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, USA.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 1:1-15.
- GARCÍA-BERTHO, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. The analysis of covariance. *Journal of Animal Ecology* 70:708-711.
- GARLAND, T., JR., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18-32.
- GREENE, H. W. 1988. Antipredator mechanisms in reptiles. Pp. 1-152. *In* C. Gans, and R. B. Huey (Eds.), *Biology of the Reptilia*. New York, USA.
- GUYER, C., AND M. A. DONNELLY. 1990. Length-mass relationship among an assemblage of tropical snakes in Costa Rica. *Journal of Tropical Ecology* 6:65-76.
- JAYNE, B. C. 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *Journal of Morphology* 172:83-96.
- JAYNE, B. C. 1988. Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. *Journal of Experimental Biology* 140:1-33.

- JAYNE, B. C., AND M. A. RILEY. 2007. Scaling of the axial morphology and gap-bridging ability of the brown tree snake (*Boiga irregularis*). *Journal of Experimental Biology* 210:1148-1160.
- JENNER, J. V., AND H. G. DOWLING. 1985. Taxonomy of American Xenodontine snakes: the tribe Pseudoboini. *Herpetologica* 41:161-172.
- KELLEY, K. C., S. J. ARNOLD, AND J. GLADSTONE. 1997. The effects of substrate and vertebral number on locomotion in the garter snake *Thamnophis elegans*. *Functional Ecology* 11:189-198.
- KING, R. B. 1989. Sexual dimorphism in snake tail length: Sexual selection, natural selection, or morphological constraint?. *Biological Journal of the Linnean Society* 38:133-154.
- KOHLSDORF, T., M. B. GRIZANTE, C. A. NAVAS, AND A. HERREL. 2008. Head shape evolution in Tropidurinae lizards: does locomotion constrain diet?. *Journal of Evolutionary Biology* 21:781-790.
- LILLYWHITE, H. B., AND R. W. HENDERSON. 1993. Behavioral and functional ecology of arboreal snakes. Pp. 1-48. *In* R. A. Seigel, and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, USA.
- LINDELL, L. E. 1994. The evolution of vertebral number and body size in snakes. *Functional Ecology* 8:708-719.
- LOSOS, J. B. 1992. The evolution of convergent community structure in Caribbean *Anolis* communities. *Systematic Biology* 41:403-420.
- MADDISON, W. P., AND D. R. MADDISON. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.7.1. Available at <http://mesquiteproject.org>.
- MARTINS, M., AND E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78-150.
- MARTINS, M., M. S. ARAÚJO, R. J. SAWAYA, AND R. NUNES. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). *Journal of Zoology (London)* 254:529-538.
- MARTINS, M., O. A. V. MARQUES, AND I. SAZIMA. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. Pp. 307-328. *In* G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- MIDFORD, P. E. T., T., JR. GARLAND, AND W. P. MADDISON. 2008. PDAP package of Mesquite. Version 1.14.

- PAGEL, M. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* 156:431-442.
- PIZZATTO, L., S. M. ALMEIDA-SANTOS, AND R. SHINE. 2007a. Life history adaptations to arboreality in snakes. *Ecology* 88:359-366.
- PIZZATTO, L., O. A. V. MARQUES, AND M. MARTINS. 2007b. Ecomorphology of boine snakes, with emphasis on South American forms. Pp. 254-269. *In* R. W. Henderson (Org.), *Biology of Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- RICHMOND, J. Q., AND T. W. REEDER. 2002. Evidence for parallel ecological speciation in Scincid lizards of the *Eumeces skiltonianus* species group (Squamata: Scincidae). *Evolution* 56:1498-1513.
- RICKLEFS, R. E., AND D. B. MILES. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pp. 13-41. *In* P. C. Wainwright, and S. M. Reilly (Eds.), *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, Chicago, USA.
- RODRIGUES, M. T. 1993. Herpetofauna of paleoquaternary sand dunes of the middle São Francisco River: Bahia: Brazil. VI. Two new species of *Phimophis* (Serpentes: Colubridae) with notes on the origin of Psammophilic adaptations. *Papéis Avulsos de Zoologia* 38:187-198.
- RODRIGUES, M. T. 2003. Herpetofauna da Caatinga. Pp. 181-236. *In* I. R. Leal, M. Tabarelli, and J. M. C. Silva (Orgs.), *Ecologia e conservação da Caatinga*. Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil.
- SCHLUTER, D., AND L. NAGEL. 1995. Parallel speciation by natural selection. *American Naturalist* 146:292-301.
- SCHLUTER, D. 2000. *The ecology of adaptative radiation*. Oxford University Press, Oxford, Oxford, UK.
- SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269-277.
- SHINE, R., M. M. OLSSON, I. T. MOORE, M. P. LEMASTER, AND R. T. MASON. 1999. Why do male snakes have longer tails than females?. *Proceedings of the Royal Society of London* 266:2147-2151.
- STATSOFT. 2005. *Statistica for Windows, Release 7.1*. T. Statsoft, Inc, Tulsa, Oklahoma, USA.
- STRÜSSMANN, C., AND I. SAZIMA. 1990. Esquadrinhar com a cauda: uma tática de caça da serpente *Hydrodynastes gigas* no Pantanal, Mato Grosso. *Memórias do Instituto Butantan* 52:57-61.

- VIDAL, N., S. G. KINDL, A. WONG, AND S. B. HEDGES. 2000. Phylogenetic relationships of Xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. *Molecular Phylogenetics and Evolution* 14:389-402.
- VIDAL, N., M. DEWYNTER, AND D. J. GOWER. 2010. Dissecting the major American snake radiation: A molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies* 333:48-55.
- VINCENT, S. E., M. C. BRANDLEY, A. HERREL, AND M. E. ALFARO. 2009. Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. *Journal of Evolutionary Biology* 22:1203-1211.
- WINEMILLER, K. O., L. C. KELSO-WINEMILLER, AND A. L. BRENKERT. 1995. Ecological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes* 44:235-261.
- ZAHER, H. 1994. Phylogenie des Pseudoboini et evolution des Xenodontinae sud-americains (Serpentes, Colubridae). P.h.D. Dissertation, Muséum National D'Histoire Naturelle, Paris, France.
- ZAHER, H., F. G. GRAZZIOTIN, J. E. CADLE, R. W. MURPHY, J. C. MOURA-LEITE, AND S. L. BONATTO. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia* 49:115-153.
- ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey, USA.

TABLE 1.— Snout-vent length (SVL), relative number of ventral scales (RNVs), Relative number of subcaudal scales (RNsc), Relative body circumference (RBC), head shape, and microhabitat use (Mic, proportion of individuals found in activity on vegetation) of pseudoboa snakes. SD = Standard deviation; N = sample size. Morphological data multiplied by 1000, except SVL.

	SVL ($\bar{x} \pm DP$)	N	RNVs ($\bar{x} \pm DP$)	N	RNsc ($\bar{x} \pm DP$)	N	RCirc ($\bar{x} \pm DP$)	N	Head shape ($\bar{x} \pm DP$)	N	Mic
<i>Boiruna maculata</i>	1102 $\pm$ 135	29	196 $\pm$ 23	29	305 $\pm$ 23	26	74 $\pm$ 8	28	628 $\pm$ 94	25	-
<i>Clelia clelia</i>	1625 $\pm$ 413	6	140 $\pm$ 28	6	-	-	79 $\pm$ 5	5	-	-	0.07
<i>Clelia plumbea</i>	1403 $\pm$ 189	27	159 $\pm$ 19	26	373 $\pm$ 47	23	74 $\pm$ 8	24	582 $\pm$ 92	23	0.00
<i>Clelia rustica</i>	889 $\pm$ 87	21	234 $\pm$ 22	21	292 $\pm$ 16	20	83 $\pm$ 10	20	556 $\pm$ 52	20	-
<i>Drepanoides anomalus</i>	470 $\pm$ 45	10	355 $\pm$ 27	10	454 $\pm$ 38	9	76 $\pm$ 6	10	510 $\pm$ 33	9	0.15
<i>Mussurana bicolor</i>	509 $\pm$ 33	7	338 $\pm$ 26	7	396 $\pm$ 15	7	88 $\pm$ 4	7	496 $\pm$ 26	6	-
<i>Mussurana quimi</i>	757 $\pm$ 82	20	257 $\pm$ 29	20	382 $\pm$ 22	20	87 $\pm$ 7	21	544 $\pm$ 75	20	-
<i>Oxyrhopus clathratus</i>	717.15 $\pm$ 78	20	280 $\pm$ 30	20	392 $\pm$ 17	20	63 $\pm$ 5	20	506 $\pm$ 45	20	0.00
<i>Oxyrhopus guibei</i>	672.4 $\pm$ 103	20	290 $\pm$ 51	20	406 $\pm$ 22	20	71 $\pm$ 7	20	531 $\pm$ 44	19	0.05
<i>Oxyrhopus melanogenys</i>	524 $\pm$ 91	27	372 $\pm$ 72	26	430 $\pm$ 27	26	73 $\pm$ 9	27	523 $\pm$ 60	27	0.03
<i>Oxyrhopus petola</i>	771 $\pm$ 59	24	264 $\pm$ 18	21	472 $\pm$ 27	21	68 $\pm$ 6	21	520 $\pm$ 54	22	0.03
<i>Oxyrhopus rhombifer</i>	512.5 $\pm$ 57	20	362 $\pm$ 32	20	356 $\pm$ 42	20	77 $\pm$ 8	18	495 $\pm$ 48	20	0.04
<i>Oxyrhopus trigeminus</i>	523.3 $\pm$ 85	21	365 $\pm$ 41	21	375 $\pm$ 28	21	75 $\pm$ 10	21	517 $\pm$ 41	21	0.00
<i>Phimophis guerini</i>	656.8 $\pm$ 128	23	314 $\pm$ 64	23	356 $\pm$ 36	22	85 $\pm$ 11	22	558 $\pm$ 66	23	0.00
<i>Phimophis guianensis</i>	430.4 $\pm$ 55	7	412 $\pm$ 44	7	344 $\pm$ 25	7	84 $\pm$ 12	6	638 $\pm$ 64	6	-
<i>Phimophis iglesiasi</i>	375.4 $\pm$ 36	7	449 $\pm$ 34	7	295 $\pm$ 30	7	96 $\pm$ 10	7	526 $\pm$ 47	7	-
<i>Pseudoboa coronata</i>	629.1 $\pm$ 57	20	298 $\pm$ 28	19	504 $\pm$ 20	19	76 $\pm$ 8	19	572 $\pm$ 54	18	0.00
<i>Pseudoboa haasi</i>	902.6 $\pm$ 88	20	220 $\pm$ 22	20	404 $\pm$ 18	20	81 $\pm$ 8	20	560 $\pm$ 40	20	0.00
<i>Pseudoboa neuwiedii</i>	636.3 $\pm$ 80	13	289 $\pm$ 36	12	439 $\pm$ 28	12	85 $\pm$ 10	10	529 $\pm$ 38	10	0.11
<i>Pseudoboa nigra</i>	813.6 $\pm$ 110	20	252 $\pm$ 29	20	495 $\pm$ 25	20	85 $\pm$ 10	20	565 $\pm$ 37	20	0.07
<i>Rhachidelus brazilii</i>	982.3 $\pm$ 63	25	182 $\pm$ 12	25	452 $\pm$ 25	21	108 $\pm$ 13	20	586 $\pm$ 50	23	-
<i>Siphlophis cervinus</i>	604.2 $\pm$ 54	18	419 $\pm$ 35	18	456 $\pm$ 21	18	54 $\pm$ 6	18	566 $\pm$ 44	17	0.64
<i>Siphlophis compressus</i>	633.1 $\pm$ 90	21	386 $\pm$ 51	21	477 $\pm$ 21	21	54 $\pm$ 5	20	585 $\pm$ 47	21	0.29
<i>Siphlophis longicaudatus</i>	710.9 $\pm$ 74	20	314 $\pm$ 31	19	479 $\pm$ 31	18	53 $\pm$ 8	20	569 $\pm$ 54	18	-

<i>Siphlophis pulcher</i>	604.2 ± 55	16	384 ± 34	15	471 ± 24	14	57 ± 8	16	538 ± 44	12	0.25

Fig. 1. Reconstruction of semi-arboreal habits in pseudoboine snakes. White branches represent non-arboreal habits and black branches, semi-arboreal.

Fig. 2. Mean (middle point), standard errors (boxes), and standard deviations (vertical bars) of snout-vent length (SVL) of pseudobovine snakes. Fillings in the boxes refer to different clades. The known semi arboreal species are underlined and SVL values are transformed into their natural log.

Fig. 3. Reconstruction of snout-vent length (SVL) in pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Fig. 4. Mean (middle point), standard errors (boxes), and standard deviations (vertical bars) of the relative number of subcaudal scales (RNsc) of pseudoboinae snakes. Fillings in the boxes refer to different clades. The known semi arboreal species are underlined and RNsc values are transformed into the arcsine of their square root.

Fig. 5. Reconstruction of the relative number of subcaudal scales (RNsc) in pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Fig. 6. Mean (middle points), standard errors (boxes), and standard deviations (vertical bars) of the relative body circumference (RBC) of pseudoboine snakes. Fillings in the boxes refer to different clades. The known semi-arboreal species are underlined and RBC values are transformed into the arcsine of their square root.

Fig. 7. Mean (middle point), standard errors (boxes), and standard deviations (vertical bars) of head shape of pseudoboine snakes. Fillings in the boxes refer to different clades. The known semi-arboreal species are underlined and head shape values are transformed into the arcsine of their square root.

Fig. 8. Reconstruction of head shape in pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Fig. 9. Mean (middle point), standard errors (boxes), and standard deviations (vertical bars) of the relative number of ventral scales (RNvs) of pseudoboinae snakes. Fillings in the boxes refer to different clades. The known semi-arboreal species are underlined and RNvs values are transformed into the arcsine of their square root.

Fig. 10. Reconstruction of the relative number of ventral scales (RNvs) in pseudoboine snakes. The colors of the branches represent an increase in values, from white to black.

Conclusão Geral

As serpentes da tribo Pseudoboini possuem uma dieta altamente diversificada, sendo composta principalmente de lagartos e pequenos mamíferos. Algumas espécies foram consideradas generalistas, enquanto outras apresentaram dietas especializadas (e.g. em lagartos, pequenos mamíferos, serpentes, ovos de ave e ovos de lagarto). As especializações em lagartos, pequenos mamíferos e serpentes surgiram independentemente em táxons terminais ao menos duas vezes ao longo da história evolutiva do grupo. As especializações em ovos de ave e ovos de lagarto surgiram cada uma em apenas um táxon terminal, sendo a primeira uma autapomorfia de *Rachidelus brazili* e a segunda provavelmente um autapomorfia de *Drepanoides anomalus*.

Em relação ao microhabitat, o presente estudo indica que pelo menos quatro espécies de pseudoboíneos podem ser consideradas semi-arborícolas e que este hábito surgiu independentemente pelo menos duas vezes durante a diversificação da tribo. Adicionalmente, o presente estudo aponta que o ancestral da tribo era, provavelmente, uma espécie não-arborícola.

Em relação aos aspectos morfológicos analisados, a robustez parece ser um caráter bastante conservativo dentro da tribo. Isto pode estar relacionado com a falta de associação entre esta, o consumo de pequenos mamíferos e a arborealidade.

O volume da cabeça é bem variável entre as espécies da tribo e não esteve associado com o consumo de pequenos mamíferos. Em contrapartida, o formato da cabeça parece ser menos variável e não esteve relacionado com a arborealidade. Dessa forma, possíveis pressões seletivas relacionadas à evolução da morfologia da cabeça nos pseudoboíneos permanecem obscuras.

Uma diminuição do tamanho corporal não esteve associada com um aumento no uso da vegetação, corroborando resultados encontrados para outros grupos de serpentes. Não foi encontrada também, relação entre o número de vértebras por unidade corporal e o uso da vegetação. Entretanto, nota-se que as espécies semi-arborícolas apresentam valores altos para esta variável, apesar da grande variação da mesma entre as espécies da tribo. Uma associação positiva entre o tamanho da cauda e a arborealidade indica que as espécies semi-arborícolas tendem a possuir caudas mais longas, concordando com outros estudos sobre ecomorfologia de serpentes.

Um ancestral com uma robustez e um volume de cabeça adequados a uma dieta baseada em pequenos mamíferos poderia estar relacionado às ausências de associações adaptativas encontradas no presente estudo. A partir disso, tanto a robustez quanto o volume da cabeça deixariam de ser limitantes para a evolução deste tipo de dieta nos pseudoboíneos. Da mesma forma, um ancestral com muitas vértebras por unidade corporal também poderia estar ligado à ausência de relação entre este aspecto morfológico e a arborealidade. Entretanto, tais hipóteses são especulativas e a inclusão futura do grupo externo nas análises ajudaria a esclarecer os resultados obtidos. Contudo, a ação de outros agentes seletivos também parece ter sido importante nestas serpentes.

A tribo Pseudoboini não apresentou várias das possíveis relações adaptativas previamente sugeridas para outros grupos de serpentes. Adicionalmente, a importância do grupo externo neste tipo de análise tornou-se evidente no presente estudo, e sua inclusão ajudará a esclarecer as possíveis relações que permaneceram duvidosas, bem como as hipóteses aqui levantadas.

Resumo Geral

As serpentes da tribo Pseudoboini apresentam grande diversidade quanto à sua ecologia, são consideradas um grupo monofilético e possuem uma filogenia conhecida. A partir disso, tornou-se possível a análise, sob um contexto evolutivo, das possíveis associações entre a morfologia e a ecologia neste grupo. Neste estudo, analisamos a dieta da tribo, bem como, testamos hipóteses de possíveis relações adaptativas entre a morfologia e a dieta e entre a morfologia e o uso do ambiente arborícola, e exploramos a evolução destes aspectos em serpentes da tribo. Nove espécies foram consideradas generalistas e 13, especialistas, sendo seis em lagartos, três em pequenos mamíferos, duas em serpentes, uma em ovos de lagarto e uma em ovos de ave. Um aumento no consumo de pequenos mamíferos, não esteve associado com um aumento da robustez e do volume da cabeça. Especializações em lagartos, pequenos mamíferos e serpentes surgiram independentemente em táxons terminais ao menos duas vezes durante a história evolutiva da tribo. A especialização em ovos de ave é uma autapomorfia de *Rhachidelus brazili*. A robustez decresceu no ancestral do gênero *Siphlophis*, e aumentou substancialmente em *R. brazili*. O tamanho da cabeça decresceu no ancestral do gênero *Siphlophis* e em *Oxyrhopus petola* e aumentou substancialmente em *Phimophis guianensis*, no ancestral de *O. trigeminus* e *O. rhombifer* e em *R. brazili*. *Siphlophis cervinus*, *S. compressus*, *S. pulcher* e *D. anomalus* foram consideradas espécies semi-arborícolas. A reconstrução do hábito semi-arborícola indica que este surgiu independentemente pelo menos duas vezes durante a diversificação do grupo. Não foram encontrados indícios de efeito da frequência do uso da vegetação sobre o tamanho do corpo, a robustez, o formato da cabeça e o número de vértebras por unidade corporal. Entretanto, o hábito arborícola parece ter levado a um aumento no tamanho da cauda. O tamanho corporal diminuiu substancialmente em *P. guianensis* e aumentou substancialmente em *Clelia rustica* e no ancestral de *C. clelia* e *C. plumbea*. Já o número de vértebras por unidade corporal diminuiu substancialmente em *C. rustica*, no ancestral de *C. clelia* e *C. plumbea*, e em *Pseudoboa haasi*; aumentou substancialmente no ancestral de *O. trigeminus* e *O. rhombifer*, e em *O. melanogenys* e *P. guianensis*. O tamanho da cauda diminuiu significativamente em *C. rustica*, *Boiruna maculata* e *P. haasi* e aumentou consideravelmente no ancestral do gênero *Siphlophis*, *O. petola*, *D. anomalus*, *R. brazili* e no ancestral do gênero *Pseudoboa*. A largura da cabeça diminuiu substancialmente em *Pseudoboa newwiedii* e aumentou substancialmente em *S. compressus*, *P. guianensis* e em *B. maculata*. As ausências de relações possivelmente

adaptativas podem estar ligadas a uma forte inércia filogenética e/ou ao efeito de outros agentes seletivos. Um ancestral morfologicamente adequado a uma dieta baseada em pequenos mamíferos e ao uso da vegetação também pode ter influenciado os resultados. O conhecimento do grupo externo da tribo Pseudoboini ajudaria a esclarecer ainda mais as relações entre morfologia e ecologia nestas serpentes.

Palavras chave: Evolução; Serpentes; Ecologia.

General Abstract

Snakes of the tribe Pseudoboini are ecological diversity, considered as a monophyletic group and have a known phylogeny. Thus, the analyses of possible associations between the morphology and the ecology of this group in an evolutionary framework became possible. In the present study, we analyze the diet of pseudoboine species, and we test hypotheses of possible adaptative relationships between morphology and diet, and between morphology and microhabitat use in pseudoboine snakes. We also explore how these traits evolved during the diversification of the tribe. Nine species were considered as diet generalists and 13, as diet specialists, being six lizard specialists, three small mammal specialists, two snake specialists, one a lizard egg specialist, and one a bird egg specialist. An increase in the consumption of small mammals was not associated with an increase in robustness and head volume. Lizard, small mammal and snake specializations occurred independently at least twice in terminal taxa during the diversification of the tribe. A specialization in bird eggs seems to be an autapomorphy of *Rhachidelus brazili*. Robustness decreased in the ancestor of *Siphlophis* species, and increased substantially in *R. brazili*. Head volume decreased in the ancestor of *Siphlophis* species and in *Oxyrhopus petola*, and increased substantially in *Phimophis guianensis*, in the ancestor of *O. trigeminus* and *O. rhombifer* and in *R. brazili*. *Siphlophis cervinus*, *S. compressus*, *S. pulcher* and *D. anomalus* were considered as semi-arboreal. The semi-arboreal habit reconstruction indicates that this habit evolved independently at least twice during the diversification of the group. We did not find indications of the effect of vegetation use on body size, robustness, head shape and the number of ventral scales per body unit. However, vegetation use seems to have led to an increase in tail length. Body size substantially decreased in *P. guianensis* and substantially increased in *Clelia rustica* and in the ancestor of *C. clelia* and *C. plumbea*. The number of vertebrae per body unit decreased substantially in *C. rustica*, in the ancestor of *C. clelia* and *C. plumbea*, and in *Pseudoboa haasi*. It substantially increased in the ancestor of *O. trigeminus* and *O. rhombifer*, and in *O. melanogenys* and *P. guianensis*. Tail length significantly decreased in *C. rustica*, *Boiruna maculata* and *P. haasi*, and increased substantially in the ancestor of the genus *Siphlophis*, in *O. petola*, *D. anomalus*, *R. brazili* and in the ancestor of *Pseudoboa* spp.. Head width decreased substantially in *Pseudoboa newwiedii* and increased significantly in *S. compressus*, *P. guianensis* and in *B. maculata*. Strong influence of phylogenetic inertia and/or the effect of alternative selective agents could be related to the absences of these possible adaptative

relationships. An ancestor with a morphology adequate to a diet based on small mammals and to arboreality could also have influenced the results. Knowing the outgroup of the tribe Pseudoboini would help to further clarify the relationships between morphology and ecology of these snakes.

Key words: Evolution; Snakes; Ecology.

Apêndices

APPENDIX I

Specimens Examined

Boiruna maculata: Instituto Butantan (IB): 1343, 1642, 1831, 2567, 4612, 4658, 4660, 4691, 4835, 5272, 8290, 8881, 9060, 9436, 9676, 9788, 10246, 13077, 15167, 15666, 15979, 16846, 17403, 19691, 20458, 20494-95, 21097, 21406, 23128, 23425, 23430, 23590, 23742, 23891, 24055, 24336, 25824, 28251, 29117, 29713, 30413-14, 30416, 30461, 30560, 30672, 32156, 33036, 33068, 34454, 40395, 40397, 41819, 42121, 42685, 42717, 49262, 49304, 49434, 50101, 50340, 50471, 51263, 52175-76, 52261, 53526, 54348, 55255, 55661, 55690, 56280, 62284, 67633. Coleção Herpetológica da Universidade de Brasília (CHUNB): 10750. Coleção Herpetológica da Puc/Rio Grande do Sul (PUCRS): 6601. ***Boiruna sertaneja***: IB: 4612, 4658-60, 4691, 9060, 13077, 20458, 21097, 33068, 49262, 49304, 49434, 50101, 50340, 51263, 52261. Museu da Universidade de São Paulo (MZUSP): 4982-83, 4994, 5842, 7034, 7036. ***Clelia clelia***: IB: 2853, 7234, 8688, 13958, 24793, 25402, 25708, 42681, 54460. CHUNB: 9673, 44846. Museu Paranense Emílio Goeldi (MPEG): 8, 20399, 21770, 22222, 22387, 23014, 23015. ***Clelia hussami***: PUCRS: 16859-60. Coleção Herpetológica do Museu Nacional Capão de Imbúia (MHNCI): 11937. ***Clelia plumbea***: IB: 153, 155, 1530, 2181, 3178-79, 3181, 3434, 3581, 4379, 4470, 6471, 7689, 8533, 8875, 9418, 9712, 9938, 10346, 15392, 17008, 19673, 19929, 21466, 21696, 21862, 21969, 21996, 22024, 22037, 22312, 22497, 22730, 22775, 23593-94, 24136, 24244, 24399, 24885, 24968, 26005, 27757, 27921, 28021, 28738, 28884, 29013, 29319, 30312, 31473, 32183, 33138, 33643, 33912, 33947, 33992, 37582, 40082, 42143, 43474, 44629, 49251, 50973, 52866, 55832. MHNCI: 4990, 10350. MPEG: 28, 423, 1643, 1802, 5715, 8036, 8375, 8435, 12015, 12299, 15056, 15057, 15597, 16641, 16740, 16820, 16989, 17133, 17199. Coleção Herpetológica da Universidade Federal do Mato Grosso (UFMT): 5957. ***Clelia rustica***: IB: 347, 1787, 1788-91, 1812, 1819, 2546, 8812, 9526, 10088, 12749, 12791, 19584, 23722, 30440, 34315, 34393, 40351, 43470-73, 45878, 47110, 47326, 49046-47, 49378, 49772, 51848, 58882. MHNCI: 898, 2735, 5346, 5361, 8484, 9647, 12336. PUCRS: 1143, 1429, 5696, 6350, 11041, 12391, 13416, 13815, 14637, 14761, 18174. ***Drepanoides anomalus***: IB: 14945-46. MPEG: 9420, 16738, 17894-95, 19259, 19395, 19457, 19975, 20274, 21114, 22392, 22484-85, 22528, 22932. MZUSP: 8723, 9350, 11190. UFMT: 1984, 3751, 3753, 3755, 3757, 7295, 7321. ***Mussurana bicolor***: IB: 4316, 4553, 4859, 6147, 6333, 7716, 9080, 9084, 10079, 10440, 12731, 14201, 14272,

15513, 16847, 24600, 25960, 32206, 37361. PUCRS: 488, 11154. UFMT: 2208, 4068, 6259, 1936, 1986. *Mussurana quimi*: IB: 380, 711, 880, 1813, 5897, 8752, 9074, 9515, 11327, 14331, 22445, 22485, 22490, 22726, 24323, 24633, 25605-06, 26906, 27442, 28257, 29461, 30029, 30242, 32031, 33039, 33062, 33131, 33216, 33572, 34293, 37255, 40380, 40747, 41066, 42616-17, 44141, 48816, 48851, 51142, 52008, 52644, 54849, 54883, 54903, 54913, 54963, 55244, 59322, 61153-54, 63873, 68459. CHUMB: 3871, 3876, 20356. *Oxyrhopus clathratus*: IB: 7125, 7833, 8600, 9279, 31062, 32955, 44106, 53835, 56346, 61100, 70616-17, 70756, 70807, 70883, 70949, 71042, 71447, 71756, 71807, 71872, 72332, 72647, 73011, 73161, 73222, 73253, 73258, 73294-95, 73360, 73406, 73431, 73994, 74269, 74619, 74653, 74739, 75178, 75206, 75624, 76744, 76745. *Oxyrhopus guibei*: IB: 14523, 14532, 15431-32, 16204, 21083, 31924, 52472, 55500, 61231, 61447, 61929, 64075, 64141, 64144-45, 64624, 64819, 64921, 64925, 67420, 67867, 69687, 69723, 69930, 70540, 70698, 70814, 70847-48, 71931, 73369-70, 73432-33, 73608, 75016, 76012, 76014, 76524. *Oxyrhopus melanogenys*: IB: 7220, 14872, 14874, 14877, 17208, 17681, 18520, 25129, 31954, 31989, 31998, 40100, 40808, 40876-78, 40890, 41471, 47047, 47082, 52718, 53442, 54179, 71643-51, 73960, 76872. MPEG: 2539, 4589, 6460, 7034, 13258, 14030, 16445, 17883, 18690, 20265, 21401. UFMT: 3817-23, 3826-29, 3832-34, 3839-52, 4214, 4231, 4240, 4873-74, 5200, 5202, 5212-13, 5485, 5712-13, 5742, 5831, 6197, 6263-66, 6312, 6552, 7020, 7024, 7055, 7095, 7117, 7353. *Oxyrhopus petola*: IB: 4513, 6020, 6080, 6102, 6845, 6883, 8517, 9357, 10027, 10051-52, 10364, 10512-13, 10553, 11014-15, 11018-20, 11395, 12434, 12931, 14324, 16697, 18269, 24175, 25062, 25318, 25358-59, 25584, 26073-74, 26555-56, 26578-80, 26580, 26582, 27412, 27759, 28267, 28596, 29062-65, 30150, 32043, 33238, 33950, 36956, 37383, 40633, 40644, 44181, 48825, 48857, 49041, 49782, 51157, 52267-68, 53939, 54117-22, 54125-28, 54130, 54429, 54435, 76924. *Oxyrhopus rhombifer*: IB: 22461, 37480, 37484, 40279, 52073, 52354, 52356, 53921, 56165, 57740, 59883, 64475, 66395, 66443, 66526, 69887, 70249, 73397, 73444, 74037, 75002, 75038, 75770-74, 7577-80, 76017, 76028-37, 76039-40, 76596, 76806. PUCRS: 148, 2084, 3402, 4811, 4965, 5190, 5408, 6582, 7945, 8394, 8853, 10758, 11200, 11505, 12159, 12313. UFMT: 933, 1208, 1445-46, 1450, 1771, 5154. *Oxyrhopus trigeminus*: IB: 9991, 14200, 14208-09, 14516-17, 14588, 15608, 17595, 22408, 33429, 37330, 43521, 43528-30, 43541, 43543, 49131, 50215, 50829, 52142, 56800, 56996, 62626, 62794, 63931, 64585, 65102, 65104-05, 65107-09, 67315, 67643, 68009, 69537-38, 71518, 74194, 75303, 75583, 76981, 77085, 77090, 77092. MZUSP: 13724, 13738. *Phimophis guerini*: IB: 140, 5793, 6780, 7395, 8982, 10086, 10507, 12245, 19093, 22676, 22976, 23387, 24116, 24280, 26973, 27522, 27985, 37434, 43463, 43973, 45731,

52295, 56083, 65013, 65339, 65573, 65831-34, 66025, 66399, 66400-02, 66407-08, 66410-12, 66820, 69990, 75011, 75492, 75588, 76043, 76044, 76344, 76345-46. CHUNB: 3794, 8885, 24562, 30728. MHNCI: 11530. MPEG: 21737. UFMT: 600. ***Phimophis guianensis***: IB: 19440-42, 69169. CHUNB: 56736. MZUSP: 2134, 2140-41, 4549, 8195, 9167-72, 9218, 9763. ***Phimophis iglesiassi***: IB: 1692, 42486, 43460, 43694, 49596, 65595. CHUNB: 41112, 50189, 50271, 52066. MPEG: 22748, 22780, 22792, 22795, 22797. ***Phimophis vitattus***: IB: 68980-82. ***Pseudoboa coronata***: IB: 31993, 74118. CHUNB: 47124, 49627. MPEG: 610, 8698, 10211, 15713, 16629, 17708, 18156, 18297, 18503, 18941, 19676, 19931, 20821, 21182, 21726, 22071, 22256, 22350, 22397, 22534, 22852, 23051. UFMT: 1245-46, 3714-19, 3721-32, 5744. ***Pseudoboa haasi***: IB: 397, 856, 1003, 1024, 1069, 1159, 1178, 1185, 1349, 1529, 2066, 2218, 6548, 6621, 6920, 7046, 7104, 7128, 7359, 7623, 7707, 7811, 8109-10, 8206, 8258, 8502, 8510, 9071, 9378, 9382, 9488, 9570, 9603-04, 12308, 13081, 15651, 16042, 17545, 18893, 24120, 24457, 24679, 26418, 29255, 30042, 31039, 33433, 34295, 40103, 45757, 51110, 52364, 54923. MHNCI: 1363, 5352, 5355-57, 5362, 8119, 9106, 9901, 11853, 12761. PUCRS: 467, 16800, 16990, 16992. ***Pseudoboa martinsi***: MZUSP: 15 (MPEG), 1036 (Instituto Nacional de Pesquisas da Amazônia - INPA), 15707, 20257, 31981 (IB). ***Pseudoboa neuwiedii***: IB: 19426, 20684, 24783, 24791, 24827, 24871, 25748, 25780, 25794, 40481, 41504, 44505, 56543-46, 56549. MPEG: 92, 19929, 20406, 21250, 21406, 21408, 21410, 22529, 22530-32, 22626, 23305-06. MZUSP: 4800, 5081, 5223, 6218, 8043, 8593, 10008, 10728. PUCRS: 8893. ***Pseudoboa nigra***: CHUNB: 28158, 45360, 50865, 50887, 52134. MHNCI: 6051, 7370, 7911, 10145, 11522. MZUSP: 2184-85, 3465, 6494, 6496, 7176, 10632, 11344, 11989-94, 11996-98, 14629, 15487, 15902, 15908, 15911, 17111, 17112-13, 17116, 17126. PUCRS: 4847-48, 8216. ***Pseudoboa serrana***: MHNCI: 7311-12. MZUSP: 5901, 10393, 22364, 29716, 30155, 52281, 54907. ***Rhachidelus brazili***: IB: 158, 303, 887, 1459, 1730, 4340, 5205, 6031, 6600, 6620, 7072, 7608, 7827, 8356, 8530, 9419, 9646, 9652, 10170, 15869, 19668, 21095, 21103, 24502, 24561-63, 27589, 29462, 29697, 30454, 30834-35, 31638, 31764, 31880, 31920, 32013-14, 32227, 32651, 32689, 33012, 33023, 33437, 33574, 33780, 37280, 41173, 42067, 46149, 46614, 46617, 49599, 50023, 50265, 50372, 51278-79, 54183, 73454, 76348. CHUNB: 3852, 25339, 42453. PUCRS: 925. ***Siphlophis cervinus***: IB: 2183, 2222, 9200, 14769, 14941-42, 14944, 17668-69, 20464, 40874, 41344, 43443, 46813, 46839, 46957, 47071, 47085, 47186-87, 47623-24, 52196. MPEG: 1109, 1564, 2672, 7165, 10103, 16163, 16347, 16431, 16726, 16747, 16922, 18479, 18496, 18688, 18847, 19512, 19743, 19834, 19951, 19997, 20034, 21289-90, 21414, 22083-84, 22086, 22146, 22294, 22422, 22639, 22832. MZUSP: 8443-44, 9178, 9404, 15276.

Siphlophis compressus: IB: 836, 984, 2226, 9536, 9784-87, 13767, 14962, 19125, 34426, 46174, 46448, 47075, 47617-19, 50229, 53003, 53004, 53124. CHUNB: 56735. MPEG: 2599, 3711, 5774, 5869, 16544, 16721, 16734, 16908-09, 16990, 17408, 18223, 18647, 19391, 19480-82, 19565, 20882, 21161, 22087-89, 22405, 22717. UFMT: 2216, 3657, 3660, 3666-67, 3669-74, 3678, 3680, 3689, 3946-47, 4062, 4868, 5174, 5493, 5951, 6044-45, 6049, 7049, 7184. ***Siphlophis leucocephalus***: IB: 9141, 73984. ***Siphlophis longicaudatus***: IB: 1557, 4550, 5255, 6898, 9520, 9727, 9777, 10075, 10485, 13179, 14252, 26863, 28222, 33948, 41183, 44259, 44319, 46181, 49206, 51991-92, 52093, 52401, 53827, 54244, 54777, 54957, 55702, 56975, 57020, 57387, 57560, 58987-88, 58997, 60612, 62562, 62674, 62709, 67334, 67365, 68053, 68907, 69178-79, 72527, 73244, 73787, 73812, 73862, 74012, 74048, 74177, 75101, 75226, 75259, 75425, 75464, 76503. MHNCI: 12501. ***Siphlophis pulcher***: IB: 7373, 10449, 15030, 17197, 22465, 22612, 24353, 33119, 33252, 41222, 42219, 42420, 42611, 43205, 43833, 44210, 45074, 45793, 46200, 47616, 51259, 51902, 53549, 54225, 54850, 54973, 55003, 55037, 55152, 55199, 55425, 56052, 56637, 56814, 57241, 57262, 57318. MHNCI: 334, 7121, 8346, 8347. MZUSP: 294-95, 2815, 3945-46, 11237, 11258. ***Siphlophis worontzowi***: IB: 29074, 42624, 53604, 55266, 56151, 56550, 56561, 67620, 71625. MHNCI: 7350, 10743. MZUSP: 11251, 11323, 11345. UFMT: 5364, 5480, 6268, 6532, 6694.

APPENDIX II

Diet Data

Boiruna maculata: GALLARDO, G. SCROCCHI, A. DI GIACOMO, AND A. GIRAUDO. 2006. *Boiruna maculata* (Mussurana, Víbora luta, mamona). Prey and predation behavior. Herpetological review 37: 349-350; HARTMANN, P. A., AND GIASSON, L. O. 2008. Répteis. Pp. 111-130. In J. J. Cherem, and M. Kammers (Orgs.), A fauna das áreas de influencia da usina hidreletrica Quebra Queixo. Editora Habilis, Erechim, Rio Grande do Sul, Brazil; LEMA, T., M. L. ARAÚJO, AND A. C. P. AZEVEDO. 1983. Contribuição ao conhecimento da alimentação e do modo alimentar de serpentes do Brasil. Comunicações do Museu de Ciências da PUCRS 26:41-121; PINTO, C., AND T. LEMA. 2002. Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). Iheringia 92:9-19; This study. ***Boiruna sertaneja***: VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. Amphibia-Reptilia 4:273-296; This study. ***Clelia clelia***: BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica 31:11-52; CAMPBELL, J. A. 1998. Amphibians and reptiles of northern Guatemala, the

Yucatán and Belize. The University of Oklahoma Press, Norman, Oklahoma, USA;

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352;

DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA.; DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; M. Martins and M. E. Oliveira unpublished data; VAUGHAN, A., AND V. RUIZ-GUTIERREZ. 2006. *Clelia clelia*. Diet. Herpetological Review 37:93-94.; STARACE, F. 1998. Guide des Serpents et Amphibiens de Guyane. IBIS Rouge Editions, Guadeloupe, Guyane; YANOSKY, A., J. DIXON, AND C. MERCOLLI. 1996. Ecology of a snake community of El Bagual Reserve, Argentina. Herpetological Natural History 4:97-110; This study. ***Clelia langeri***: REICHLE, S., AND D. EMBERT. 2005. New species of *Clelia* (Colubridae) from the Inter-Andean dry valleys of Bolívia. Journal of Herpetology 39:379-383. ***Clelia plumbea***: BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. South American Journal of Herpetology 1:102-113; CUNHA, O. R., AND F. P. NASCIMENTO. 1978. Ofídios da Amazônia X. As cobras da região leste do Pará, Belém. Museu Paraense Emílio Goeldi Publicações Avulsas 31:1-218; MARQUES, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica na Estação Ecológica Juréia-Itatins, SP. P.h.d. Dissertation. Universidade de São Paulo, São Paulo, São Paulo, Brazil; MORATO, S. A. A. 2005. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil.; PINTO, C., AND T. LEMA. 2002. Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). Iheringia 92:9-19; This study. ***Clelia rustica***: PINTO, C., AND T. LEMA. 2002. Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). Iheringia 92:9-19; VIDAL, S. C. 2002. Alimentación de los ofídios de Uruguay. Monografías de Herpetologia 6:7-127; This study. ***Drepanoides anomalus***: BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. South American Journal of Herpetology 1:102-113; CUNHA, O. R., AND F. P.

NASCIMENTO. 1978. Ofídios da Amazônia X. As cobras da região leste do Pará, Belém. Museu Paranaense Emílio Goeldi Publicações Avulsas 31:1-218; DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; DUELLMAN, W. E. 2005. Cusco Amazonico. Cornell University Press, Ithaca, New York, USA. M. Martins and M. E. Oliveira unpublished data; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paranaense Emílio Goeldi, Belém, Pará, Brazil. ***Mussurana bicolor***: YANOSKY, A., J. DIXON, AND C. MERCOLLI. 1996. Ecology of a snake community of El Bagual Reserve, Argentina. Herpetological Natural History 4:97-110; STRÜSSMANN, C. 1992. Serpentes do Pantanal de Poconé, Mato Grosso: Composição faunística, história natural e ecologia comparada. M.s.c. Dissertation. Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; M. Martins personal communication; This study. ***Mussurana montana***: FRANCO, F. L., O. A. V. MARQUES AND G. PUERTO. 1997. Two new species of colubrid snakes of the genus *Clelia* from Brazil. Journal of Herpetology 31:483-490; HARTMANN, P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, São Paulo, Brazil. ***Mussurana quimi***: FRANCO, F. L., O. A. V. MARQUES AND G. PUERTO. 1997. Two new species of colubrid snakes of the genus *Clelia* from Brazil. Journal of Herpetology 31:483-490; This study. ***Oxyrhopus clathratus***: BORGES, E. C. 2004. Análise da dieta de *Oxyrhopus clathratus* (Serpentes, Colubridae) da região metropolitana de Curitiba, Paraná, e litoral norte do Paraná. Monograph. Centro Universitário Positivo, Curitiba, Paraná, Brazil; HARTMANN, P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, São Paulo, Brazil; KUNZ, T. 2007. Diversidade, distribuição e história natural da região da grande Florianópolis, SC. Monograph. Universidade Federal de Santa Catarina, Florianópolis, Brazil; O. A. V. Marques unpublished data; MARQUES, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica na Estação Ecológica Juréia-Itatins, SP. P.h.d. Dissertation. Universidade de São Paulo, São Paulo, São Paulo, Brazil; MORATO, S. A. A. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. 2005. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil. ***Oxyrhopus guibei***: ANDRADE, R. O., AND R. A. SILVANO. 1996. Comportamento alimentar e dieta da falsa-coral *Oxyrhopus guibei* (Serpentes,

Colubridae). Revista Brasileira de Zoologia 13:143-150; DALMOLIN, P. C. 2000. Composição e história natural da comunidade de serpentes da Estação Ecológica de Jataí e outras áreas do município de Luiz Antonio, SP. M.s.c. Dissertation. Universidade Federal de São Carlos, São Carlos, São Paulo, Brazil; SAZIMA, I., AND ABE, A. S. 1991. Habits of five brazilian snakes with coral-snake pattern, including a summary of defensive tactics. Studies of Neotropical Fauna and Environment 26:159-164; F. E. Barbo unpublished data. ***Oxyrhopus melanogenys***: BITAR, Y. O. C., AND M. C. SANTOS-COSTA. 2006. Biologia reprodutiva e alimentar de *Oxyrhopus melanogenys* Tschudi, 1845, na Amazônia Oriental. Scientific Technical Report. Universidade Federal do Pará, Belém, Pará, Brazil; M. Martins and M. E. Oliveira unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; NASCIMENTO, F. P., T. C. S. ÁVILA-PIRES, AND O. R. CUNHA. 1987. Os répteis da área de Carajás, Pará, Brasil (Squamata). Boletim do Museu Paranaense Emílio Goeldi, Nova Série Zoologia 3:33-65; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil. ***Oxyrhopus occipitalis***: DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352. ***Oxyrhopus petola***: BERNARDE, P. S., AND R. A. MACHADO. 2000. *Oxyrhopus petola digitalis* (NCN). Prey. Herpetological Review 31:247-248; CUNHA, O. R., AND F. P. NASCIMENTO. 1983. Ofídios da Amazônia XIX. As espécies de *Oxyrhopus* Wagler, com uma subespécie nova, e *Pseudoboa* Schneider, na Amazônia Oriental e Maranhão (Ophidia: Colubridae). Boletim do Museu Paranaense Emílio Goeldi 1:1-42; DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; DUELLMAN, W. E. 2005. Cusco Amazonico. Cornell University Press, Ithaca, New York, USA.; L. Vitt unpublished data; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; C. Strüssmann unpublished data; This study. ***Oxyrhopus rhombifer***: ABALOS, J. W., E. C. BÁEZ, AND R. NADER. 1964. Serpentes de

Santiago Del Estero (Republica Argentina). *Acta Zoologica Lilloana*, 20:211-283; CECHIN, S. Z. 1999. História natural de uma comunidade de serpentes na região de depressão central (Santa Maria), Rio Grande do Sul, Brasil. P.h.d. Dissertation. Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; DI BERNARDO, M. 1999. História natural de uma comunidade de serpentes da borda oriental do Planalto das Araucárias, Rio Grande do Sul, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil.; LEMA, T., M. L. ARAÚJO, AND A. C. P. AZEVEDO. 1983. Contribuição ao conhecimento da alimentação e do modo alimentar de serpentes no Brasil. *Comunicações do Museu de Ciências da PUC do Rio Grande do Sul* 26:41-121; MASCHIO, G. F., M. DI BERNARDO, AND S. T. Z. CECHIN. 2003. *Oxyrhopus rhombifer rhombifer* (Falsacoral). *Diet. Herpetological Review* 34:71; MASCHIO, G. F., M. DI BERNARDO, AND J. MELCHORS. 2004. *Oxyrhopus rhombifer rhombifer*. *Diet. Herpetological Review* 35:71; RIBEIRO, R. A. K. 2007. História natural de uma taxocenose de serpentes da RPPN Acurizal, borda oeste do Pantanal, Serra do Amolar, Corumbá, Mato Grosso do Sul, Brasil. M.s.c. Dissertation. Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil; SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; VIDAL, S. C. 2002. Alimentación de los ofidios de Uruguay. *Monografias de Herpetologia* 6:7-127. ***Oxyrhopus trigeminus***: L. R. V. Alencar unpublished data; ÁVILA-PIRES, T. C. 1995. Lizards of Brazilian Amazônia (Reptilia: Squamata). *Zoologische Verhandelingen* 299:1-706; CUNHA, O. R., AND F. P. NASCIMENTO. 1983. Ofidios da Amazônia XIX. As espécies de *Oxyrhopus* Wagler, com uma subespécie nova, e *Pseudoboa* Schneider, na Amazônia Oriental e Maranhão (Ophidia: Colubridae). *Boletim do Museu Paranaense Emílio Goeldi* 1:1-42; DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; ROCHA, C. F. D, H. G. BERGALLO, F. H. HATANO, AND M. VAN SLUYS. 2005. *Oxyrhopus trigeminus*. (False Coral Snake). *Prey. Herpetological Review* 36:458-459.; C. Strüssmann unpublished data; VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* 4:273-296; This study. ***Oxyrhopus vanidicus***: DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication, University of Kansas, Museum of Natural History* 65:1-352. ***Phimophis guerini***: SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation,

Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; R. J. Sawaya and J. P. Miranda unpublished data; This study. *Phimophis iglesi*: C. Nogueira personal communication. *Phimophis scriptorcibatus*: RODRIGUES, M. T. 1993. Herpetofauna of paleoquaternary sand dunes of the middle São Francisco River: Bahia: Brazil. VI. Two new species of *Phimophis* (Serpentes: Colubridae) with notes on the origin of psammophilic adaptations. Papéis Avulsos de Zoologia 38:187-198. *Pseudoboa coronata*: BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica 31:11-52; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; M. A. Sena unpublished data; This study. *Pseudoboa haasi*: ESTEVES, F. A. D. 2005. Estudo da dieta e da reprodução de *Pseudoboa haasi* (Serpentes, Colubridae, Xenodontinae, Pseudoboini). Monograph. Universidade Positivo, Curitiba, Paraná, Brazil; MORATO, S. A. A. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. 2005. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil; This study. *Pseudoboa martinsi*: MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150. *Pseudoboa neuwiedii*: MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA.; This study. *Pseudoboa nigra*: GUEDES, T. B. 2006. Estrutura da comunidade de serpentes de uma área de Caatinga do Nordeste Brasileiro. M.s.c. Dissertation. Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil; RIBEIRO, R. A. K. 2007. História natural de uma taxocenose de serpentes da RPPN Acurizal, borda oeste do Pantanal, Serra do Amolar, Corumbá, Mato Grosso do Sul, Brasil. M.s.c. Dissertation. Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil; R. Orofino unpublished data; VANZOLINI, P. E., A. M. RAMOS-COSTA, AND L. J. VITT. 1980. Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro, Rio de Janeiro, Brazil; This study. *Rhachidelus brazili*: O. A. V. Marques unpublished data; P. H. Valdujo unpublished data. *Siphlophis cervinus*: CUNHA, O. R., AND F. P. NASCIMENTO. 1993. Ofídios da Amazônia. As cobras da região leste do Pará. Boletim do Museu Paraense

Emílio Goeldi, 9:1-191; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; M. Martins and M. E. Oliveira unpublished data; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; G. F. Maschio unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; NASCIMENTO, F. P., T. C. S. ÁVILA-PIRES, AND O. R. CUNHA. 1987. Os répteis da área de Carajás, Pará, Brasil (Squamata). Boletim do Museu Paranaense Emílio Goeldi, Nova Série Zoologia 3:33-65; PRUDENTE, A. L. C., MOURA-LEITE, J. C., AND S. A. A. MORATO. 1998. Alimentação das espécies do gênero *Siphlophis* (Serpentes, Colubridae). Revista Brasileira de Zoologia 15:375-383; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil. ***Siphlophis compressus***: DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; M. Martins and M. E. Oliveira unpublished data; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150.; G. F. unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; L. J. Vitt unpublished data. ***Siphlophis leucocephalus***: PRUDENTE, A. L. C., MOURA-LEITE, J. C., AND S. A. A. MORATO. 1998. Alimentação das espécies do gênero *Siphlophis* (Serpentes, Colubridae). Revista Brasileira de Zoologia 15:375-383. ***Siphlophis longicaudatus***: PRUDENTE, A. L. C., MOURA-LEITE, J. C., AND S. A. A. MORATO. 1998. Alimentação das espécies do gênero *Siphlophis* (Serpentes, Colubridae). Revista Brasileira de Zoologia 15:375-383; This study. ***Siphlophis pulcher***: DUARTE, M. R., AND M. A. SENA. 2007. *Siphlophis pulcher* (NCN). Prey. Herpetological Review 38:211; HARTMANN, P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de

Mesquita Filho, São Paulo, São Paulo, Brazil; O. A. V. Marques unpublished data; PRUDENTE, A. L. C., MOURA-LEITE, J. C., AND S. A. A. MORATO. 1998. Alimentação das espécies do gênero *Siphlophis* (Serpentes, Colubridae). *Revista Brasileira de Zoologia* 15:375-383; SAZIMA, I., AND A. J. ARGÔLO. 1994. *Siphlophis pulcher* (NCN). *Prey. Herpetological Review* 25:126; This study. *Siphlophis worontzowi*: BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. *South American Journal of Herpetology* 1:102-113; PRUDENTE, A. L. C., MOURA-LEITE, J. C., AND S. A. A. MORATO. 1998. Alimentação das espécies do gênero *Siphlophis* (Serpentes, Colubridae). *Revista Brasileira de Zoologia* 15:375-383; This study.

APPENDIX III

Microhabitat Data

Clelia clelia: DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication, University of Kansas, Museum of Natural History* 65:1-352; DUELLMAN, W. E. 2005. *Cusco Amazonico*. Cornell University Press, Ithaca, New York, USA; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78-150; G. F. Maschio unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paranense Emílio Goeldi, Belém, Pará, Brazil; MURPHY, J. C. 1997. *Amphibians and reptiles of Trinidad & Tobago*. Krieger Publishing Company, Malabar, Florida, USA; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil. *Clelia plumbea*: ARGÔLO, A. J. S. 2004. As serpentes dos cacauais do sudeste da Bahia. *Editus, Ilhéus, Bahia, Brazil*; BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. *South American Journal of Herpetology* 1:102-113;

HARTMANN, P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, São Paulo, Brazil; MARQUES, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica na Estação Ecológica Juréia-Itatins, SP. P.h.d. Dissertation. Universidade de São Paulo, São Paulo, São Paulo, Brazil; MORATO, S. A. A. 2005. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil; M. A. de Sena unpublished data. *Drepanoides anomalus*: BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. South American Journal of Herpetology 1:102-113; M. A. Carvalho unpublished data; CARVALHO, M. A. 2006. Composição e história natural de uma comunidade de serpentes em área de transição Amazônia-Cerrado, ecorregiões florestas de Mato Grosso, Município de Claudia, Mato Grosso. Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; VANZOLINI, P. E. 1986. Levantamento herpetológico da área do estado de Rondônia sob a influência da rodovia BR 364. Relatório de Pesquisa. Polonoroeste/Ecologia Animal/CNPq, Brasília, Brazil; VIDAL, N., J. MASSARY, AND C. MARTY. 1999. Nouvelle espèces de serpents pour La Guyane Française. Revue Française d' Aquariologie Herpetologie 25:131-134; YUKI, R. N., U. GALATTI, AND R. A. T. ROCHA. 1999. Contribuição ao conhecimento da fauna de Squamata de Rondônia, Brasil, com dois novos registros. Boletim do Museu Paranaense Emílio Goeldi, 15:181-193. *Oxyrhopus clathratus*: DI BERNARDO, M., M. BORGES-MARTINS, R. B. OLIVEIRA, AND G. M. F. PONTES. 2007. Taxocenoses de serpentes de regiões temperadas do Brasil. Pp. 222-263. In L. B. Nascimento, and M. E. Oliveira (Eds), Herpetologica no Brasil II. Sociedade Brasileira de Herpetologia, Belo Horizonte, Minas Gerais, Brazil; HARTMANN,

P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, São Paulo, Brazil; HARTMANN, P. A., AND GIASSEN, L. O. 2008. Répteis. Pp. 111-130. In J. J. Cherem, and M. Kammers (Orgs.), A fauna das áreas de influencia da usina hidreletrica Quebra Queixo. Editora Habilis, Erechim, Rio Grande do Sul, Brazil; KUNZ, T. 2007. Diversidade, distribuição e história natural da região da grande Florianópolis, SC. Monograph. Universidade Federal de Santa Catarina, Florianópolis, Brazil; MARQUES, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica na Estação Ecológica Juréia-Itatins, SP. P.h.d. Dissertation. Universidade de São Paulo, São Paulo, São Paulo, Brazil; S. A. A. Morato personal communication; MORATO, S. A. A. 2005. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil.

Oxyrhopus guibei: SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; SAZIMA, I., AND ABE, A. S. 1991. Habits of five brazilian snakes with coral-snake pattern, including a summary of defensive tactics. Studies of Neotropical Fauna and Environment 26:159-164; SAZIMA, I., AND C. F. B. HADDAD. 1992. Répteis da Serra do Japi: notas sobre história natural. PP. 212-236. In L. P. C. Morellato (Ed.). História Natural da Serra do Japi: Ecologia e preservação de uma área florestal no sudeste do Brasil. Editora da Unicamp/FAPESP, Campinas, São Paulo, Brazil; C. Strüssmann unpublished data; P. H. Valdujo unpublished data; Data obtained from the herpetological Collection of Universidade Federal do Mato Grosso.

Oxyrhopus melanogenys: M. A. Carvalho unpublished data; CARVALHO, M. A. 2006. Composição e história natural de uma comunidade de serpentes em área de transição Amazônia-Cerrado, ecorregiões florestas de Mato Grosso, Município de Claudia, Mato Grosso. Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; S. A. A. Morato personal communication; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; M. A. de Sena unpublished data; C. Strüssmann unpublished data; Data obtained from the Herpetological collection of Universidade Federal do Mato Grosso.

Oxyrhopus petola: CARVALHO, C. M., J. C. VILAR, AND F. F. OLIVEIRA. 2005. Répteis e anfíbios. Pp. 39-61. In C.

M. Carvalho, and J. C. Vilar (Coords), Parque Nacional Serra de Itabaiana – Levantamento Biota. Biologia Geral e Experimental, IBAMA, Aracajú, Sergipe, Brazil; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA; ESQUEDA, L. F., E. LA MARCA, AND P. SORIANO. 2005. Partial albinism in a venezuelan specimen of false coral snake *Oxyrhopus petola petola* (Linnaeus, 1758). Herpetotropicos 2:114; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA; PEREIRA-FILHO, G. A. 2007. Composição faunística de uma taxocenose de serpentes de um remanescente de Floresta Atlântica da Paraíba, Brasil. M.s.c. Dissertation. Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil; C. Strüssmann unpublished data; TEST, F. H., O. J. SEXTON, AND H. HEATWOLE. 1966. Reptiles of Rancho Grande and vicinity, estado Aragua, Venezuela. Miscellaneous Publications, University of Michigan, Museum of Zoology, 128:1-68; P. H. Valdujo unpublished data. *Oxyrhopus rhombifer*: S. A. A. Morato personal communication; R. Ribeiro unpublished data; RIBEIRO, R. A. K. 2007. História natural de uma taxocenose de serpentes da RPPN Acurizal, borda oeste do Pantanal, Serra do Amolar, Corumbá, Mato Grosso do Sul, Brasil. M.s.c. Dissertation. Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil; SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; C. Strüssmann unpublished data; P. H. Valdujo unpublished data; Data obtained from the Herpetological collection of Universidade Federal do Mato Grosso. *Oxyrhopus trigeminus*: J. C. L. Costa personal communication; PEREIRA-FILHO, G. A. 2007. Composição faunística de uma taxocenose de serpentes de um remanescente de Floresta Atlântica da Paraíba, Brasil. M.s.c. Dissertation. Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil; ROCHA, C. F. D, H. G. BERGALLO, F. H. HATANO, AND M. VAN SLUYS. 2005. *Oxyrhopus trigeminus*. (False Coral Snake). Prey. Herpetological Review 36:458-459; M. A. Sena unpublished data; C. Strüssmann unpublished data; P. H. Valdujo unpublished data. *Phimophis guerini*: LEMA, T. 1994. Lista comentada dos répteis ocorrentes no Rio Grande do Sul, Brasil. Comunicações do Museu de Ciências e Tecnologia da Puc do Rio Grande do Sul, Série Zoologia 7:41-150; S. A. A. Morato personal communication; SAWAYA, R. J. 2003. História natural e ecologia das serpentes de cerrado da região de Itirapina, SP. P.h.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; C. Strüssmann unpublished data; P. H. Valdujo unpublished data; Data

obtained from the Herpetological collection of Universidade Federal do Mato Grosso.

Pseudoboa coronata: BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31:11-52; P. S. Bernarde unpublished data; M. A. Carvalho unpublished data; CARVALHO, M. A. 2006. Composição e história natural de uma comunidade de serpentes em área de transição Amazônia-Cerrado, ecorregiões florestas de Mato Grosso, Município de Claudia, Mato Grosso. Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78-150; M. A. Sena unpublished data; SILVA JR, N. J. DA. 1996. The snakes from Samuel Hydroelectric Power Plant and vicinity, Rondônia, Brazil. *Herpetological Natural History* 1:37-86; F. Stender personal communication. ***Pseudoboa haasi***: R. Bérnills and G. Montingelli unpublished data; R. Bérnills and E. M. Wistuba unpublished data; G. V. Bianconi and C. E. Conte unpublished data; KUNZ, T. 2007. Diversidade, distribuição e história natural da região da grande Florianópolis, SC. Monograph. Universidade Federal de Santa Catarina, Florianópolis, Brazil; S. A. A. Morato personal communication; MORATO, S. A. A. 2005. Serpentes da região atlântica do estado do Paraná, Brasil: Diversidade, distribuição e ecologia. P.h.d. Dissertation. Universidade Federal do Paraná, Curitiba, Paraná, Brazil; E. J. Sanches personal communication. ***Pseudoboa neuwiedii***: BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31:11-52; M. Hoogmoed personal communication; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78-150; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA; F. Sarnento personal communication.

Pseudoboa nigra: CARVALHO, C. M., J. C. VILAR, AND F. F. OLIVEIRA. 2005. Répteis e anfíbios. Pp. 39-61. In C. M. Carvalho, and J. C. Vilar (Coords), Parque Nacional Serra de Itabaiana – Levantamento Biotá. Biologia Geral e Experimental, IBAMA, Aracajú, Sergipe, Brazil; GUEDES, T. B. 2006. Estrutura da comunidade de serpentes de uma área de Caatinga do Nordeste Brasileiro. M.s.c. Dissertation. Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil; M. A. Sena unpublished data; C. Strüssmann unpublished data; STRÜSSMANN, C. 1992. Serpentes do Pantanal de Poconé, Mato Grosso: Composição

faunística, história natural e ecologia comparada. M.s.c. Dissertation. Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; Data obtained from the Herpetological collection of Universidade Federal do Mato Grosso. *Siphlophis cervinus*: DIXON, J. R., AND P. SOINI. 1986. The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, USA; DUELLMAN, W. E. 2005. Cusco Amazónico, the lives of amphibian and reptiles in an Amazonian rainforest. Cornell University Press, Ithaca, New York, USA; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; G. F. Maschio unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paranense Emílio Goeldi, Belém, Pará, Brazil; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; M. A. Sena unpublished data; F. Stender personal communication. *Siphlophis compressus*: BERNARDE, P. S. 2004. Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil. P.h.d. Dissertation. Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; BERNARDE, P. S. AND A. S. ABE. 2006. A snake community at Espigão do Oeste, Rondônia, Southwestern, Brazil. South American Journal of Herpetology 1:102-113; M. A. Carvalho unpublished data; CARVALHO, M. A. 2006. Composição e história natural de uma comunidade de serpentes em área de transição Amazônia-Cerrado, ecorregiões florestas de Mato Grosso, Município de Claudia, Mato Grosso. Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, University of Kansas, Museum of Natural History 65:1-352; MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78-150; G. F. Maschio unpublished data; MASCHIO, G. F. 2008. História natural e ecologia das serpentes da Floresta Nacional de Caxiuanã, Melgaço/Portel, Pará, Brasil. P.h.d. Dissertation. Museu Paranense Emílio Goeldi, Belém, Pará, Brazil; S. A. A. Morato personal communication; MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad & Tobago. Krieger Publishing Company, Malabar, Florida, USA; SANTOS-COSTA, M. C. 2003. História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxiuanã, Melgaço, Pará. P.h.d. Dissertation. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; M. A. Sena unpublished data; YUKI, R. N., U. GALATTI, AND R. A. T.

ROCHA. 1999. Contribuição ao conhecimento da fauna de Squamata de Rondônia, Brasil, com dois novos registros. Boletim do Museu Paranaense Emílio Goeldi, 15:181-193. *Siphlophis pulcher*: P. Gobbo and C. Conti unpublished data; HARTMANN, P. A. 2005. História natural e ecologia de duas taxocenoses de serpentes na Mata Atlântica. P.h.d. Dissertation. Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, São Paulo, Brazil; O. A. V. Marques unpublished data; MARQUES, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica na Estação Ecológica Juréia-Itatins, SP. P.h.d. Dissertation. Universidade de São Paulo, São Paulo, São Paulo, Brazil; SAZIMA, I., AND A. J. ARGOLO. 1994. *Siphlophis pulcher* (NCN). Prey. Herpetological Review 25:126; F. M. Teixeira unpublished data.