

# The Evolution of Diet and Microhabitat Use in Pseudoboine Snakes

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**Abstract.** Reflecting their exceptional radiation, snakes occur in different habitats and microhabitats and are able to eat numerous types of prey. The availability of good and comprehensive phylogenies for different snake's lineages together with natural history data provides an opportunity to explore how ecological traits diversified during their radiation. In the present study, we describe the diet and microhabitat variation (arboreal or non-arboreal) in the tribe Pseudoboini and explore how these traits evolved during the tribe's diversification. We analyzed specimens deposited in scientific collections and gathered information on diet and microhabitat use available in the literature and provided by other researchers. We also mapped diet and microhabitat data onto a phylogeny of the tribe using the principle of parsimony. Pseudoboine snakes feed mainly on lizards and small mammals, and 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 highly diverse feeding habits of pseudoboines seem to have evolved mainly in the terminal taxa. Among those species that had enough microhabitat data (17 species), *Drepanoides anomalus*, *Siphlophis cervinus*, *S. compressus*, and *S. pulcher* frequently use the vegetation. Our results indicate that an increase in arboreality evolved several times during the diversification of the tribe, and that the *Siphlophis* clade seems to have maintained the high degree of arboreality from its ancestor. Species that frequently use vegetation are either lizard or lizard egg specialists, indicating that these habits might be associated in the evolution of pseudoboines.

**Keywords.** Dipsadidae; Diversity; Specialization; Arboreality.

**Resumo.** Como reflexo de sua radiação excepcional, as serpentes são encontradas em diferentes habitats e microhabitats e são capazes de consumir vários tipos de presa. A disponibilidade de filogenias bem resolvidas para diversas linhagens de serpentes em conjunto com dados de história natural para estes grupos, fornecem uma oportunidade para se explorar como esses aspectos ecológicos diversificaram ao longo da sua evolução. No presente estudo, descrevemos a variação da dieta e do microhabitat (se arbórea ou não) para as serpentes da tribo Pseudoboini e exploramos como esses dois aspectos evoluíram durante a diversificação do grupo. Analisamos espécimes depositados em coleções científicas e compilamos informações sobre a dieta e o uso do microhabitat disponíveis na literatura e disponibilizadas por pesquisadores. Adicionalmente, mapeamos a dieta e o uso do microhabitat em uma filogenia da tribo por meio do princípio da parcimônia. As serpentes da tribo Pseudoboini alimentam-se principalmente de lagartos e pequenos mamíferos. Em 22 espécies para as quais um número mínimo de registros de presa foi obtido, nove são generalistas, seis são especialistas em lagartos, três em pequenos mamíferos, dois em serpentes, um é especialista em ovos de lagartos e um em ovos de ave. Essa diversidade de hábitos alimentares parece ter surgido principalmente nos ramos terminais. Dentre as espécies que apresentaram um número mínimo de observações de microhabitat (17 espécies), *Drepanoides anomalus*, *Siphlophis cervinus*, *S. compressus* e *S. pulcher* frequentemente utilizam a vegetação. Os resultados indicam que o grau de arborealidade aumentou diversas vezes durante a diversificação da tribo, e que um alto grau de arborealidade foi mantido do seu ancestral no gênero *Siphlophis*. Todas as espécies que frequentemente utilizam a vegetação são especialistas em ovos de lagarto ou em lagartos, o que sugere que estes hábitos devem estar associados na evolução da tribo Pseudoboini.

## INTRODUCTION

Snakes represent one of the most exceptional radiations on earth, as shown by their great number of species (around 2900, Vitt and Caldwell, 2009) and worldwide distribution (Lillywhite and Henderson, 1993; Greene, 1997). Due to the unique morphology that evolved in these organisms (e.g., an elongation of the body and the loss of the limbs, Gans, 1961), snakes exhibit striking adaptations, especially in their feeding apparatus (Gans, 1961; Gans, 1983; Pough and Groves, 1983; Greene, 1997).

This group comprises gape-limited predators with a highly modified skull that shows the greatest degree of cranial kinesis observed among vertebrates (for details see Gans, 1961; Lee *et al.*, 1999; Cundall and Greene,

2000). These impressive modifications allowed snakes to eat numerous prey types of different sizes (Greene, 1997) and appear to lie at the heart of their successful radiation (Pough and Groves, 1983). Therefore, snakes can be found in almost all types of habitats with the exception of polar regions and the deep sea (Greene, 1997). In consequence, there are terrestrial, arboreal, fossorial, cryptozoic and aquatic snakes that vary greatly in the degree of specialization in each of these microhabitat categories (e.g., Martins *et al.*, 2001; Pizzatto *et al.*, 2007). Moreover, diet and microhabitat seem to be tightly correlated in snakes, and the evolution of one may impose several limitations on the evolution of the other in different groups of organisms (e.g., Savitzky, 1983; Motta *et al.*, 1995; Martins *et al.*, 2001; Kohlsdorf *et al.*, 2008).

Therefore, exploring the diversity of ecological traits and how they evolved in snakes may result in significant insights into the general patterns found in this group. Additionally, uncovering patterns may also enable exploration of the processes that generated them. Here we provide a description of diet and microhabitat variation (arboreal or non-arboreal) in the tribe Pseudoboini (Bailey, 1967; Serpentes: Dipsadidae) and explore how these traits evolved during their diversification.

The Neotropical snake tribe Pseudoboini appears to be monophyletic (Zaher *et al.*, 2009; Grazziotin *et al.*, 2012), with 47 species comprising the genera *Boiruna*, *Clelia*, *Drepanoides*, *Mussurana*, *Oxyrhopus*, *Phimophis*, *Pseudoboa*, *Rhachidelus* and *Siphlophis*. Recently, Grazziotin *et al.* (2012) proposed the genera *Paraphimophis*, that contains *P. rusticus* (former *Clelia rustica*), and *Rodriguesophis*, that contains *R. iglesiasi*, *R. chui* and *R. scriptorbatus* (previously included in the genus *Phimophis*). Pseudoboine snakes occur from México to Argentina (Uetz, 2011; Gaiarsa *et al.*, in press) and are highly diverse both in morphological and ecological aspects (*e.g.*, Martins and Oliveira, 1998; Pizzatto, 2005, Gaiarsa *et al.*, in press). Scattered information concerning their feeding habits (*e.g.*, Andrade and Silvano, 1996; Martins and Oliveira, 1998; Prudente *et al.*, 1998; Orofino *et al.*, 2010) indicates that most species eat mainly lizards and small mammals, with some more specialized on lizards. Oophagy and ophiophagy have been recorded occasionally for some species of the tribe (see Vitt and Vangilder, 1983; Prudente *et al.*, 1998; Pinto and Lema, 2002), and *Drepanoides anomalus* is considered a lizard egg specialist (Martins and Oliveira, 1998). Most pseudoboine 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* and *Rodriguesophis* spp.) (Cunha and Nascimento, 1978, 1983; Martins and Oliveira, 1998; Marques *et al.*, 2001; Marques *et al.*, 2005; Bernarde and Abe, 2006).

## MATERIALS AND METHODS

### Diet data

We analyzed the diet of 33 species of pseudoboines by examining the digestive tracts of 871 preserved specimens and by gathering literature data and observations granted by other researchers (see Gaiarsa *et al.*, in press). 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 snake 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 was used only for those species for which at least eight prey records were available (see Analyses; Table 1), since we consider that a smaller number of individual records might not be enough to characterize the diet of a given species.

### Microhabitat data

Information on microhabitat use was obtained from the literature, scientific collections, and observations reported by other researchers (see Gaiarsa *et al.*, in press). Only 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 microhabitat observations were available, using the same rationale used for the number of individual prey records to characterize diet. Here, microhabitat data are used as a proportion of microhabitat use (proportion of individuals found active on vegetation; Martins *et al.* 2001; Table 1).

### Analyses

Diet and arboreality information were optimized on the most recent and comprehensive published phylogenetic hypothesis for the tribe Pseudoboini (Grazziotin *et al.*, 2012) using the Mesquite software (Maddison and Maddison, 2009) based on the principle of parsimony with branch lengths set to one (Garland *et al.*, 1992). We used Fitch parsimony (non-additive or unordered states; Fitch, 1971) to reconstruct diet (categorical) and the Wagner or linear parsimony to reconstruct arboreality (continuous; see Hardy, 2006, for a detailed explanation on parsimony reconstructions). We placed species that were not included in the original phylogeny based on their phylogenetic affinities with the species that were already included (*e.g.*, Martins *et al.*, 2001; Martins *et al.*, 2002) using information from the literature and provided by other researchers with experience in this snake group (*e.g.*, Zaher, 1994; Vidal *et al.*, 2000; Zaher *et al.*, 2009; H. Zaher, *pers. comm.*). We did not include an outgroup due to uncertainty about the sister group of Pseudoboini (Vidal *et al.*, 2000; Zaher *et al.*, 2009; Vidal *et al.*, 2010; H. Ferrarezzi, *pers. comm.*). The optimization of diet was done using discrete characters (*e.g.*, lizard specialist, generalist) and arboreality was reconstructed using continuous characters (proportion of individuals found active on vegetation). Pseudoboine species that did not have enough observations (eight or more) for both diet and microhabitat are shown in Table 1 and 2 but were not included in the character reconstruction. Species that had eight or more observations for one trait but not for the other were included in the character reconstruction.

**Table 1.** Proportion of prey items recorded for pseudoboine snakes; *N* = total number of items.

	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>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>Paraphimophis rusticus</i>	0.50	0.10	0.40						10
<i>Phimophis guerini</i>	0.08	0.92							12
<i>Pseudoboa coronata</i>	0.27	0.45	0.18					0.09	11
<i>Pseudoboa haasi</i>	0.60	0.13	0.20					0.07	15
<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>Rodriguesophis iglesiasi</i>		1							3
<i>Rodriguesophis scrittorcibatus</i>		1							2
<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

Reconstruction of categorical states in Mesquite allows the inclusion of species with missing data and provides the most parsimonious state for them. However, continuous methods in Mesquite do not allow missing data (Hofmann *et al.*, 2006), and the resulting arboreality states for *Siphlophis longicaudatus*, *Mussurana quimi*, *Paraphimophis rusticus*, *Boiruna maculata*, *B. sertaneja* and *Rhachidelus brazili* are unknown. We did not prune them from the phylogeny to provide a better visualization of the character reconstruction (see Results and Fig. 1).

## RESULTS

Of the 32 species for which we obtained any diet data (Table 1), 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 the species that presented lizard or bird eggs as part of their diet, lizards and birds, respectively, were also consumed.

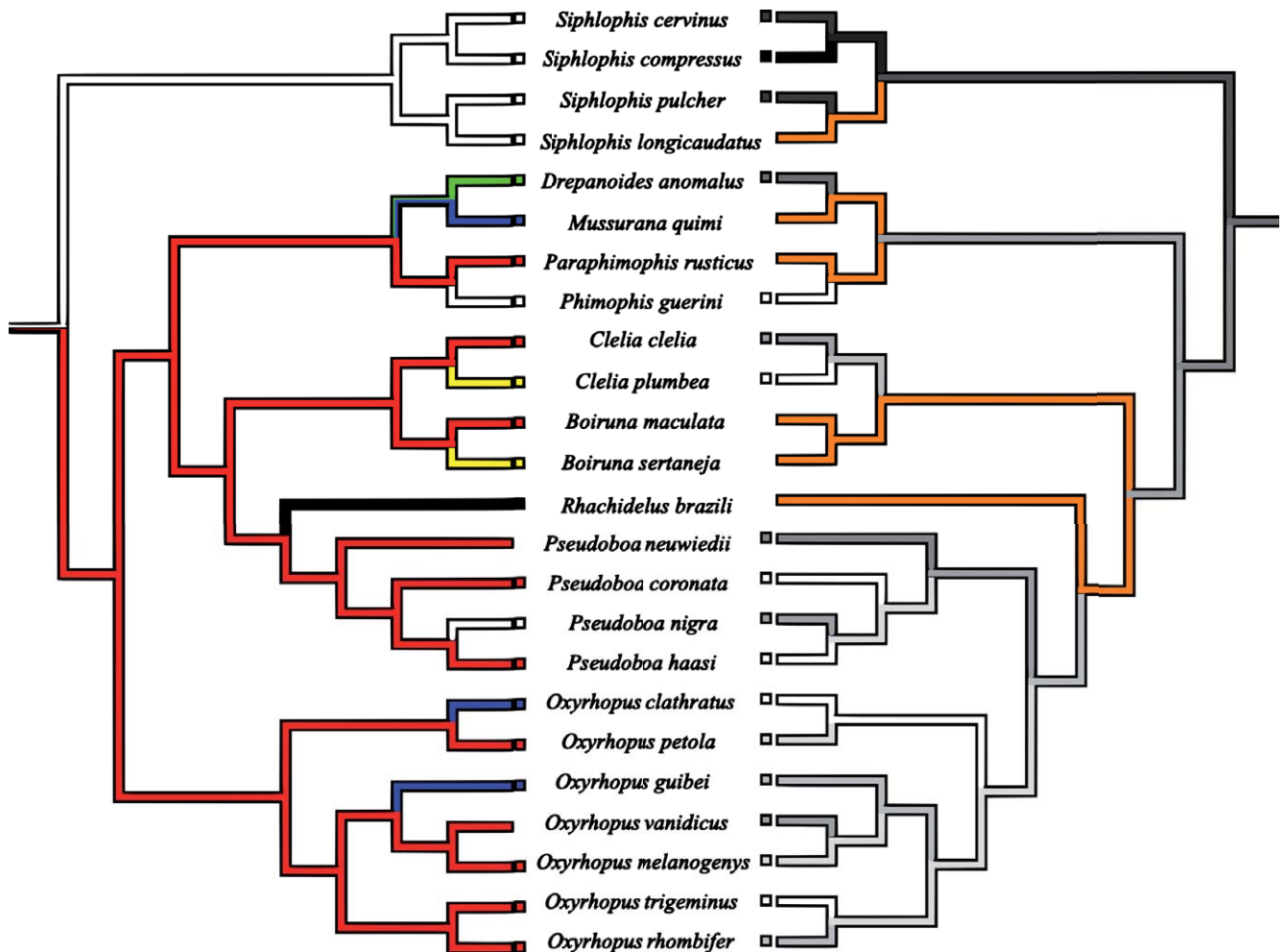
We obtained eight or more prey records for 22 species. Of these, nine were considered as generalists, *i.e.*, no prey represented more than 70% of the total: *Boiruna maculata*, *Clelia clelia*, *Oxyrhopus melanogenys*, *O. petola*, *O. rhombifer*, *O. trigeminus*, *Paraphimophis rusticus*, *Pseudoboa 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, once 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.

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 (assuming that the ancestor had a distinct diet). Specialization in small mammals (*O. clathratus*, *O. guibei* and *M. quimi*) and in snakes (*B. sertaneja* and *C. plumbea*) also appeared each independently at least twice during the diversification of the tribe. The bird egg specialization is an autapomorphy of *R. brazili* and lizard egg specialization is probably an autapomorphy of *D. anomalus*, but since the diet reconstruction of the immediate ancestor of this species shows an equivocal branch, we are uncertain about it. Diet optimization indicates that *Pseudoboa newwiedii* and *Oxyrhopus vanidicus* are probably generalist species, but we were able to gather

only four and six observations respectively regarding their diet and this categorization remains uncertain.

In relation to microhabitat use (Table 2), among those species that had enough microhabitat data (eight or more observations; 18 species), *Drepanoides anomalus*, *Siphlophis cervinus*, *S. compressus*, and *S. pulcher* frequently use the vegetation, *Clelia clelia*, *Pseudoboa newwiedii*, *P. nigra*, and *Oxyrhopus vanidicus* occasionally use it, and *Oxyrhopus guibei*, *O. melanogenys*, *O. petola*, and *O. rhombifer* seem to rarely use it. The remaining species do not explore the arboreal microhabitat (Table 2). It is evident that the degree of arboreality increased several times during the diversification of the tribe and that the *Siphlophis* clade seems to have maintained the high degree of arboreality from its ancestor (Fig. 1). An even higher degree of arboreality evolved in *Siphlophis compressus* and it seems to be the most arboreal pseudoboine among the species analyzed. Our reconstruction indicates that the ancestor of pseudoboines frequently used the vegetation, and that



**Figure 1.** Reconstruction of diet (left) and arboreality (right) in pseudoboine snakes. In the left cladogram branches colors are as follow: white = lizard specialists, red = generalists, green = lizard egg specialists, blue = small mammal specialists, yellow = snake specialists, and black = bird egg specialists. Branches colors in the right cladogram represent an increase in arboreality from white to black. Orange branches represent ambiguous states. Branches with no boxes at the end represent species that do not have enough data on the underlying ecological trait.

**Table 2.** Proportion of arboreal and non arboreal observations recorded for pseudoboine snakes; *N* = total number of microhabitat observations.

	Arboreal observations	Non arboreal observations	N
<i>Boiruna maculata</i>	0.17	0.83	6
<i>Boiruna sertaneja</i>		1	1
<i>Clelia clelia</i>	0.07	0.93	15
<i>Clelia plumbea</i>		1	8
<i>Drepanoides anomalus</i>	0.15	0.85	26
<i>Mussurana bicolor</i>		1	4
<i>Mussurana quimi</i>		1	2
<i>Oxyrhopus clathratus</i>		1	27
<i>Oxyrhopus guibei</i>	0.05	0.95	21
<i>Oxyrhopus melanogenys</i>	0.03	0.97	30
<i>Oxyrhopus occipitalis</i>		1	1
<i>Oxyrhopus petola</i>	0.03	0.97	34
<i>Oxyrhopus rhombifer</i>	0.04	0.96	53
<i>Oxyrhopus trigeminus</i>		1	26
<i>Oxyrhopus vanidicus</i>	0.06	0.94	17
<i>Paraphimophis rusticus</i>		1	2
<i>Phimophis guerini</i>		1	12
<i>Rodriguesophis iglesiasi</i>		1	3
<i>Pseudoboa coronata</i>		1	24
<i>Pseudoboa haasi</i>		1	8
<i>Pseudoboa martinsii</i>		1	1
<i>Pseudoboa neuwiedii</i>	0.11	0.89	9
<i>Pseudoboa nigra</i>	0.07	0.93	15
<i>Rhachidelus brazilii</i>		1	5
<i>Siphlophis cervinus</i>	0.64	0.36	14
<i>Siphlophis compressus</i>	0.29	0.71	34
<i>Siphlophis leucocephalus</i>		1	4
<i>Siphlophis longicaudatus</i>	0.50	0.50	2
<i>Siphlophis pulcher</i>	0.25	0.75	12
<i>Siphlophis worontzowi</i>	0.50	0.50	4

arboreality increased even more in the ancestor of the species of *Siphlophis* (Fig. 1).

## 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*, from ectothermic to endothermic prey (*i.e.*, lizards to small mammals). However in the present study, in *O. guibei* more than 70% of the diet consists of small mammals and only 21% of lizards. This suggests that juveniles also feed on endothermic prey. On the other hand, we cannot rule out the possibility that our sample has underestimated the diet of juveniles and therefore has caused a bias in our results. Because we used considerable diet data from the literature and the majority of these authors did not provide information regarding the stage of maturity of the specimens (e.g., newborn,

juvenile or adult) we were unable to investigate the presence of an ontogenetic shift in diet for pseudoboine snakes. Nevertheless, diet data on other species of the genus *Oxyrhopus* (*O. melanogenys*, *O. petola*, *O. rhombifer*, *O. trigeminus*) reveal a similar proportion between endo and ectothermic prey and suggest that this shift may occur in other pseudoboines, as observed in pitvipers of the genus *Bothrops* (Martins *et al.*, 2002).

Ophiophagy was occasionally reported 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. Like in the present study, Pinto and Lema (2002) 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, as well in *Phimophis guerini* and in *Pseudoboa nigra*, and also a specialization in lizard eggs in *Drepanoides anomalus*, as already reported in the literature (e.g., Martins and Oliveira, 1998; Prudente *et al.*, 1998; Sawaya, 2003; Orofino *et al.*, 2010).

Pseudoboines have diverse feeding habits and most of this diversification seems to have occurred in the terminal taxa. Through the reconstruction of the evolutionary history of diet, it seems that the ancestors of the 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. Since 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 *Drepanoides anomalus* and *Rachidelus brazilii* may have favored the emergence of egg specialization in these species.

Among pseudoboines, *Drepanoides anomalus* and the species of *Siphlophis* are known to be semi-arboreal (e.g., Martins and Oliveira, 1998; Marques *et al.*, 2001), which is in accordance with our study. We suggest that *S. longicaudatus* may also use the vegetation based on its slender body and long tail (e.g., Martins *et al.*, 2001; Pizzatto *et al.*, 2007). However, we were unable to gather enough microhabitat observations for this species to better characterize its microhabitat use. Surprisingly, *Clelia clelia*, *Pseudoboa neuwiedii*, *P. nigra*, and *Oxyrhopus vanidicus* also use the vegetation although in a smaller degree. The evolution of a higher degree of arboreality in the genus *Siphlophis* and in *Drepanoides anomalus*, species known to

inhabit primarily forested habitats (e.g., Duellman, 1978; Martins and Oliveira, 1998; Starace, 1998; Bernarde and Abe, 2006; but see Alencar *et al.*, 2009 and Guedes *et al.*, 2011), corroborates the hypothesis that more arboreal snakes tend to evolve more frequently in forests (Lillywhite and Henderson, 1993).

The comparison of diet and microhabitat reconstructions (Fig. 1) shows that species that frequently use the vegetation are either lizard or lizard egg specialists, indicating that these habits might be associated in the evolution of pseudoboines. On the other hand, all the other specialists and even generalists do not use the vegetation or occasionally/rarely use it. Because a more arboreal environment imposes physical limitations on snake morphology (e.g., a more slender body, Lillywhite and Henderson, 1993; Martins *et al.* 2001), a conflict with the morphological adaptations required to eat certain types of prey may arise (for example, increased stoutness to eat relatively larger prey like small mammals; Martins *et al.* 2002). A diet based on lizards or lizard eggs may overcome this conflict.

Although there are some inspiring attempts to reconstruct the evolution of diet in snakes as a whole (e.g., Gans, 1961; Greene and Burghardt, 1978; Cundall and Greene, 2000), relatively few attempts were made to uncover the evolution of diet at finer scales (e.g., in snake families, tribes or genera; e.g., Greene, 1989; Rodriguez-Robles and Jesus-Escobar, 1999; Martins *et al.*, 2002). A similar trend is evident regarding microhabitat use in snakes (e.g., Martins *et al.*, 2001). These studies are only possible with a large amount of basic natural history data associated with good, comprehensive phylogenies. Thus, although detailed systematic studies have become increasingly available for many snake lineages in the last decades (e.g., Kelly *et al.*, 2003; Lawson *et al.*, 2005; Vidal *et al.*, 2007; Zaher *et al.*, 2009; Pyron *et al.*, 2010; Grazziotin *et al.*, 2012), an increase in the number of natural history studies would allow for a better description of patterns and the exploration of processes in the evolutionary history of snakes (cf. Greene, 2005).

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